ENVIRONMENTAL VARIABLES INFLUENCING SPATIAL AND TEMPORAL PATTERNS OF FISH SPAWNING AND RECRUITMENT

FISOKUHLE LUNGILE MBATHA

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Supervisor: **Assoc. Prof. Coleen Moloney (University of Cape Town)**
Co-Supervisors: **Dr. Marek Ostrowski (Institute for Marine Research, Bergen, Norway)**
Dr. Marek Lipinski (Rhodes University and SAIAB)

DECLARATION

I hereby declare that this dissertation represents my own work. With respect to data collection, I did not participate in the surveys; all the samples were collected at sea during the Nansen surveys. Marek Ostrowski and Marek Lipinski provided data on fish abundance (hake data) and from CTD sampling arranged during the Nansen surveys. Rebecca Rademeyer provided the recruitment estimate data of both Cape hake species for this study. Additional physical data (wind speed) were extracted from ASCAT and QuikSCAT, where Dr Marek Ostrowski assisted me. The results of Chapter 2 are all based on published outputs and literature findings of previous studies. I have not allowed, and will not allow, anyone to copy my work with the intention of passing it off as his or her own work. This project is a contribution to SCAMPI, a project with the SANCOOP programme, forming a three-year bilateral research partnership between South Africa and Norway. The aim of SCAMPI was to create an interdisciplinary investigation of seasonal and decadal changes affecting marine productivity in both regions.

Signed by candidate

08/06/2017

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Signature: Miss F. L. Mbatha

Date

CONTENTS

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ABSTRACT

Spawning times and spawning intensity during the life cycles of some fish species found off South Africa and Norway were synthesized using data collected from the literature. The comparison of temporal patterns in spawning of South African fish species showed variable spawning times and intensity depending on the environmental conditions within that spawning habitat. Their spawning migration durations were suggested to be short since they inhabit a dynamic coastal upwelling ecosystem with intra-seasonal differences caused by changes in upwelling strength enhanced by south-easterly winds, nutrient-limited waters on the spawning grounds and stable thermal conditions. This contrasts with Norwegian fish species, which showed patterns of spawning times and durations that are restricted and confined to spring (February – May), probably due to strong, consistent seasonality, depending on primary production. This explains the inter-annual differences observed in their spawning periods, where strong south-westerly winds (downwelling), light intensity and salinity stratification could influence long spawning migrations. For Cape hakes, environmental variability influencing recruitment was further investigated on the west coast nursery grounds of the southern Benguela, particularly for deep-water Cape hake (*Merluccius paradoxus*). Biophysical characteristics of the west coast nursery grounds were assessed in relation to distribution of deep-water Cape hake juveniles (< 15 cm) using physical data (CTD, alongshore wind speed anomalies) and biological data (abundance/density of hake juveniles, recruitment estimates). Distinct spatial patterns of hake distribution were evident in relation to near-bottom environmental factors (temperature, salinity and oxygen). Nansen surveys conducted from 2003 – 2013 during summer (January – February) showed greater abundance of hake juveniles over the Orange Banks than in other nursery areas. The hake juveniles occurred in mid-shelf waters with oxygen depletion (2 – 3 mL $O_2.L^{-1}$) and hypoxic conditions (< 2 mL $O_2.L^{-1}$) and temperature ranges of 7 – 11 ºC. Salinity appeared to have less influence on hake juveniles' distribution. During spring

surveys, hake catches were reduced on all nursery grounds except near Cape Columbine. There was a strong positive correlation between deep-water Cape hake recruitment indices and summer wind speed anomalies for the same year (Lag = 0 year) and with autumn wind speed anomalies of the previous year (Lag = 1 year). The relationship between winds and near-bottom oxygen concentrations on the Orange Banks is unclear and needs to be investigated.

GENERAL INTRODUCTION

Coastal upwelling ecosystems are important, ecologically dynamic marine environments that support many of the world's largest and most important fisheries (FAO, 1995). They are among the most productive ecosystems and contribute approximately 50 % of the world's fisheries landings. Variability in wind strength and direction create an extremely dynamic pattern in the coastal ecosystems (Hill et al., 1998). As the wind blows along the coastline, surface waters are pushed offshore and bottom waters that are cold and rich in nutrients are brought to the surface. This supports primary production and a food chain from prey to predator animals (including fish populations). As the coastal upwelling ecosystems support large productive fisheries, it is important to understand the influences of oceanographic conditions on annual and decadal fluctuations in fish populations (Bakun et al., 2015). Small pelagic and demersal fish communities that inhabit coastal upwelling ecosystems are required to deal with a variety of major physical factors, including increases in upwelling strength, offshore advection, near-surface stratification, and hypoxic conditions (Bakun et al., 2015). Therefore, comparing the spatial and temporal patterns of small pelagic and demersal fish species from coastal upwelling ecosystems (especially for their life history events) to other marine environments will contribute to knowledge about the effects of oceanographic variability on fish, particularly during reproduction processes.

Chapter 1: Early life stages and recruitment success of fish in the southern Benguela upwelling ecosystem

Fish species in the southern Benguela ecosystem

Small pelagic fish species and demersal fish species that inhabit the coastal upwelling ecosystem of southern Africa are among the most socio-economically valuable fish stocks. The small pelagic fish species include sardine (*Sardinops sagax*) and anchovy (*Engraulis encrasicolus*), as well as round herring (*Etrumeus whiteheadi*) and Cape horse mackerel (*Trachurus capensis*), the latter two being by-catch species (Hutchings et al., 1998; Huggett et al., 2003). The demersal trawl fish species that are commercially targeted by the demersal fishery are two Cape hake species, deep-water hake (*Merluccius paradoxus*) and shallow-water hake (*Merluccius capensis*) (Grote et al., 2007; Grote et al., 2012). These species are heavily exploited in their marine ecosystem and can be affected by fluctuations in physical dynamics of the marine environment (van der Lingen et al., 2001; Hutchings et al., 2002).

One of the systems that supports rich fish fauna of these species is the Benguela Current Large Marine Ecosystem (BCLME), which is one of the four eastern boundary upwelling ecosystems (Figure 1.1) in the world's ocean (Hill et al., 1998). The BCLME is a unique upwelling system driven by large-scale wind patterns and thermohaline forcing (Fennel, 1999) and ecologically supports dynamic and large plankton productivity (Hutchings et al., 2002). The Benguela oceanographic dynamics are not the only mechanisms influencing fish species; food availability and predator-prey interactions also play their roles in this ecosystem. However, it is important to link the physical properties of this ecosystem to the spatial and temporal variability of fish species.

Oceanography of the southern Benguela upwelling ecosystem

The cold Benguela system is situated off the wide south-western shelf of Africa (Figure 1.1) and is bounded by the warm Agulhas current in the south at 34°S and warm Angolan waters to the north at 10°N (Shillington, 1998). It is characterized by strong coastal upwelling predominantly linked to equatorward winds and associated with cold sea surface temperatures (SSTs) (Miller et al., 2006, Rubio et al., 2009). The Benguela upwelling system is subdivided into northern and southern regions. The Lüderitz upwelling cell located off the coast of Namibia from 26.6°S to 28°S is the largest upwelling cell in the Benguela and separates the northern Benguela and southern Benguela upwelling ecosystems (Cury and Shannon, 2004).

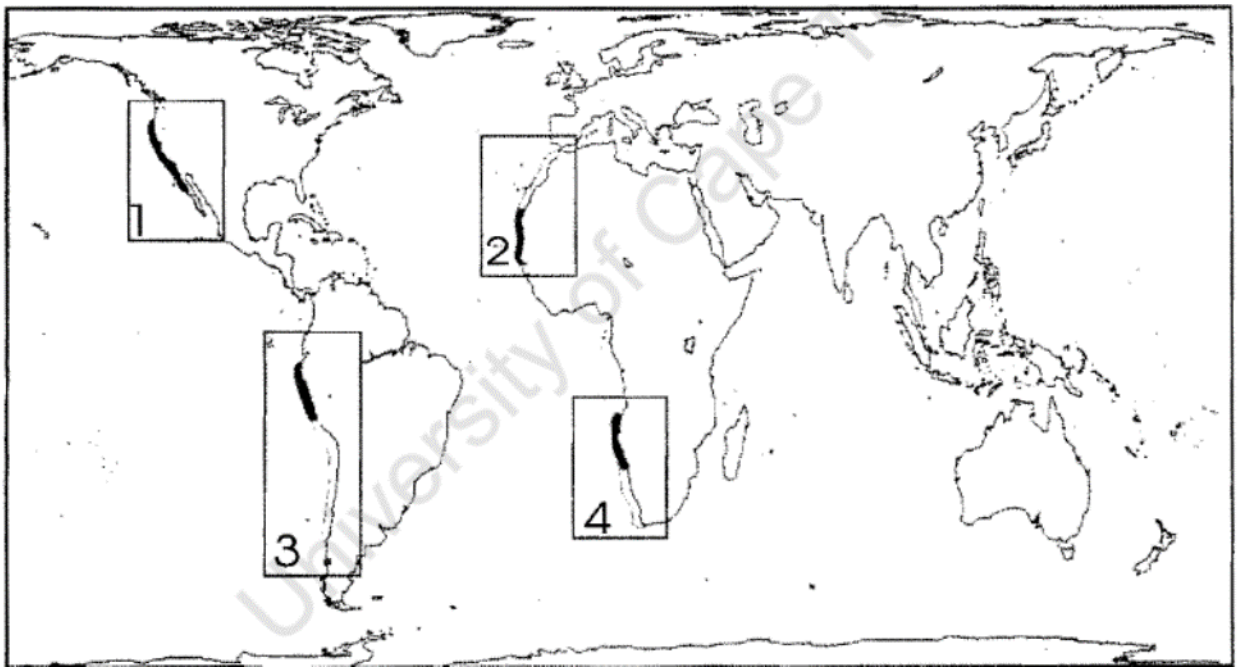

Figure 1.1: Four eastern boundary current systems of the world indicated by rectangular boxes showing major upwelling ecosystems (1) California Current system, (2) Canary Current system, (3) Humboldt Current system and (4) Benguela Current system (extracted from Jarre-Teichmann and Christensen, 1998).

The southern Benguela region (Figure 1.2) is located off the south-west coast of South Africa, extending northwards from 35°S to 28°S (Mullon et al., 2003) and is characterized by a strong surface coastal current that flows northward along the continental shelf break (Shannon et al., 1996). This strong coastal current is directly linked to the seasonal variability of cross-shelf temperature gradients created by the upwelling of cold nutrient-rich waters on the shelf and the warm waters offshore (Shillington, 1998). This coastal upwelling region is forced by Ekman offshore transport of surface waters driven by the south-easterly winds that blow during austral summer (Hill et al., 1998). The southern Benguela shelf circulation is influenced by short-term and intra-seasonal fluctuations of these upwelling-favourable winds (Hutchings et al., 2009). The main features driving this dynamic circulation include the warm Agulhas Current (Figure 1.2) along the south coast, the coastal jet flowing northwards along the Cape Peninsula shelf and mesoscale structures such as filaments, plumes, and eddies (Shillington et al., 2006). Coastal upwelling is a prominent feature along the south coast between Cape Agulhas and Cape Point (Fennel, 1999). However, it is not as intense as the west coast upwelling because of reduced variability of atmospheric forcing such as wind stress, which weakens in winter and intensifies in summer (Shannon et al., 1996; Hutchings et al., 1998).

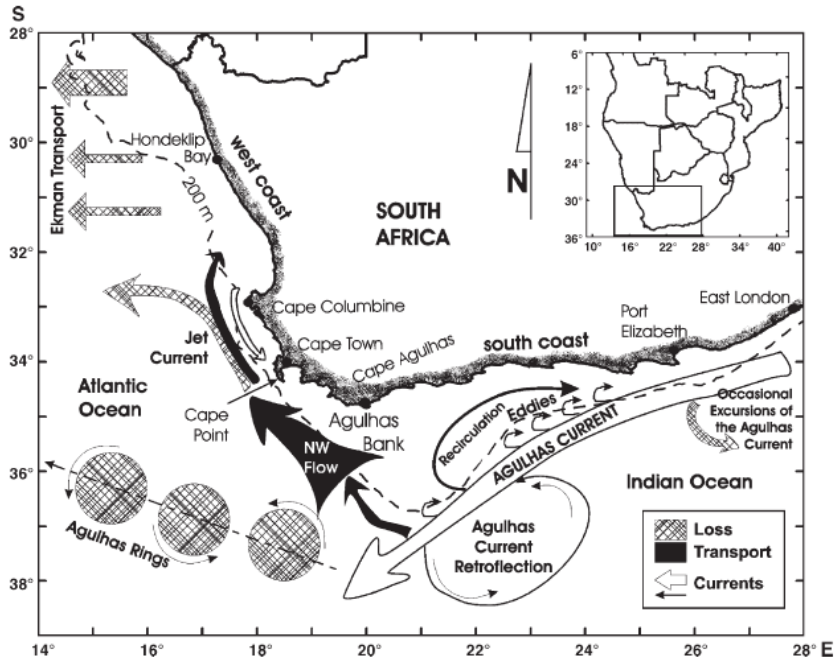

Figure 1.2: Map showing hydrographical conditions as well as aspects of the circulation in the southern Benguela ecosystem affecting the transport, retention and loss of small pelagic eggs and larvae (extracted from Boyd et al., 1992; Hutchings et al., 2002).

These oceanographic processes in the southern Benguela are influential throughout the life cycles of small pelagic and demersal fish species that are heavily targeted in this ecosystem. As these fish species (sardine, anchovy, round herring, Cape horse mackerel and two Cape hakes) mainly inhabit surface, near-surface and near-bottom waters over the continental shelf along the west and south coast regions (van der Lingen and Huggett, 2003; Grote et al., 2007), they are influenced by physical mechanisms in the southern Benguela. The influence of oceanographic dynamics during fish life cycles differs depending on the early life stages. The small pelagic and demersal fish life cycles involve early life history events that are important for their complex reproductive processes. These early life history events comprise spawning (in which adult fish release eggs), hatching (in which larvae emerge from eggs), and transport of eggs and larvae to nursery grounds and recruitment of juvenile fish to the fishery (Hutchings et al., 2002; Petitgas et al., 2010). All these

key life history events have their own average durations, which are generally at intra-annual scales (i.e. within time scales of less than one year). These key events are often associated with habitats that are interconnected (Petitgas et al., 2010) and hence, it is challenging to study the early life stages of fish species and their variability in time and space (Hutchings et al., 2002). Knowledge regarding early life stages of many fish species is still poor. Spawning of small pelagic and demersal fish species found in the southern Benguela tends to be reasonably well understood compared to other key life history events. Spawning completes the life cycle when adult fish migrate from feeding grounds to spawning grounds (Parada et al., 2008). This life cycle closure can be affected when environmental factors influence the links between the habitats of successive life history events (Parada et al., 2008).

Spawning time and space of small pelagic and demersal fish species

The Agulhas Bank is the main spawning ground found off the southern Benguela upwelling ecosystem for most southern African small pelagic and demersal fish species. It is a broad, warm continental shelf extension located to the south of southern Africa (Figure 1.2). It extends from Cape Point in the west to East London in the east (Hutchings et al., 2002) and is subdivided into the western (18 ˚E – 20 ˚E), central (20 ˚E – 22.5 ˚E) and eastern Agulhas Bank (22.5 ˚E – 28.5 ˚E) (van der Lingen et al., 2001; Twatwa et al., 2005). Spawning occur in a variety of ways in fish populations and may depend on changes in environmental factors of local grounds (Ellertsen et al. 1989). Some fish species can release multiple eggs throughout the year (i.e. they are serial spawners) while others can release multiple eggs throughout the season (i.e. they are batch spawners).

Anchovy spawn serially on the western Agulhas Bank between September and February, peaking during mid-summer (November – December) (Shelton, 1986; van der Lingen and Huggett, 2003). Anchovy are mostly distributed in a temperature ranges of 16 to 19°C (Hutchings et al., 1992) and the spawning success of anchovy in the southern Benguela is thought to be regulated by temperature, with temperature fluctuations directly influencing spawning duration (Shelton, 1986). Since 1994, there have been shifts in the spawning distribution on the east-central Agulhas Bank and these were related to temperature changes (Roy et al., 2007). Sardine spawn throughout the year but mainly have two spawning peaks, in early spring and autumn (van der Lingen and Huggett, 2003) and they have large temperature ranges from 14.5 to 21.5°C in their spawning areas to the west of Cape Point (Fowler, 1998). They also use the east coast for spawning (Twatwa et al., 2005).

Cape horse mackerel spawn over the eastern/central Agulhas Bank (Hutchings et al., 2002). The spawning period of Cape horse mackerel in South African waters varies over the spawning grounds of the Agulhas Bank, where it appears to have two major spawning peaks during winter and summer (Barange et al., 1998). Contradictions in Cape horse mackerel spawning times and location are documented in Hecht (1990), who found that spawning peaks are in June and November on the eastern Agulhas Bank, while Naish (1990) found that the main spawning period is during August and February on the western Agulhas Bank.

The round herring spawning period is between July and November over the eastern Agulhas Bank (van der Lingen, 1998). The spawning of round herring seems to occur for prolonged periods and multiple frequencies (Roel and Melo, 1990).

Demersal fish species that are abundant in the southern Benguela region are shallow-water Cape hake and deep-water Cape hake (Grote et al., 2007, Grote et al., 2012, Jansen et al., 2015) and both are batch and serial spawners. There are two separate spawning populations of shallow-water hake, in Namibia and on the Agulhas Bank (Jansen et al., 2015). Deep-water hake mainly spawn in South African waters (Crawford et al., 1980; Grote et al., 2007; Strømme et al., 2015). The horizontal dispersal of eggs and the size distribution of larvae of deep-water hake indicate a substantial number of these individuals are likely released on the western Agulhas Bank and only a small fraction spawn offshore of St. Helena Bay (33°S). Deep-water hake spawn all year round with highest spawning activities from August to October, while shallow-water hake spawn in spring and summer (September – March) (Shelton, 1986, Grote et al., 2007).

Long-term variability in spawning time and duration has been suggested to be driven by climate effects such as changes in upwelling intensity, water temperature and oxygen concentration (van der Lingen et al., 2006). Hutchings et al. (2009) described the change in wind patterns as one of the major effects influencing the two sub-regions of the Benguela upwelling ecosystem. This can lead to delays or early timing of key life history events in fish life cycles (Roy et al., 2007). Understanding the range and overlap between adult spawning grounds, juvenile nursery grounds and potential environmental mechanisms influencing each of these habitats is important for understanding fish population dynamics (Boyer et al., 2001).

Biophysical characteristics of west coast nursery grounds

As there is an interconnection between adult spawning grounds and juvenile nursery grounds in the southern Benguela ecosystem, biophysical characteristics are important for recruitment success. Recruitment is a phase where the number of fish in the annual fish stock survives until they enter the early life stage of post-larval to reach maturity and this phase occurs in the nursery

grounds after spawning. However, recruitment differs between small pelagic and demersal fish species of the southern Benguela. Small pelagic fish eggs and larvae are transported by a jet current from the spawning ground on the Agulhas Bank to the west coast nursery grounds (Boyer et al., 2001). There are thought to be two major nursery grounds (St. Helena Bay and the Agulhas Bank) in the southern Benguela ecosystem (van der Lingen and Huggett, 2003). Each nursery ground is linked to a spawning area, a transport or recirculation mechanism, potential alongshore or cross-shelf transport and a productive area resulting from coastal or shelf-edge upwelling (Hutchings et al., 2009).

As the Agulhas Bank is both a spawning ground and a nursery area (van der Lingen and Huggett, 2003), the cyclonic shelf eddies generated on the western Agulhas Bank tend to modulate recruitment success as they are responsible for advection of eggs and larvae towards the coastal Benguela jet (Huggett and Mullon, 2003). The eggs of fish species spawning on the nutrient-poor Agulhas Bank are carried to nutrient-rich inshore nursery grounds on the west coast (Hutchings et al., 2002). Distributions of fish eggs and larvae in the southern Benguela have undergone large fluctuations in both small pelagic and demersal fish species, resulting from variability in physical environmental variables (Boyer et al., 2001). However, the migration evidence for demersal fish species in the southern Benguela remains poorly understood, especially in reaching nursery grounds for recruitment. Both Cape hake species have pelagic eggs and larvae that are transported passively to nursery grounds, where conditions are good for survival (Grote et al., 2012). The Namibian and South African spawning populations of shallow-water hake share their nursery grounds on the west coast (Grote et al., 2007; Jansen et al., 2015). There is one known nursery area for deep-water hake, which is located over the shelf off the Orange River mouth, whereas shallow-water hake nursery areas appear to be located just north of St Helena Bay (Grote et al.,

2012). The findings from Lagrangian modelling of eggs and larvae in the southern Benguela suggest that the two species follow different drift routes from spawning locations separated by depth (Stenevik et al., 2008; Garavelli et al., 2012). Additional evidence for different nursery areas is provided by abundance distribution maps for deep-water Cape hake (Le Clus et al., 2005a) and shallow-water Cape hake (Le Clus et al., 2005b). Deep-water Cape hake juveniles (i.e. individuals smaller than 16 cm in length size) are usually found further offshore than shallow-water Cape hake juveniles.

There is spatial and temporal variability in the abundance of the early life stages of the two Cape hake species (Grote et al., 2012). The number of fish larvae that survive during migration and succeed in reaching retention areas can determine the annual recruitment to fish stocks for local fisheries (Bakun, 1998). Several hypotheses have been proposed to explain the roles of biophysical interactions in fish life cycles with an emphasis on recruitment. In this study, the focus will be on two hypotheses Cury and Roy's (1989) "optimal environmental window hypothesis" explained a domed-shaped relationship between recruitment and wind speed in upwelling areas. Intermediate wind speeds were considered optimal, being strong enough to allow sufficient upwelling to support prey production and weak enough to prevent losses by advection away from coastal feeding grounds. To explain recruitment variability in association with environmental factors, Bakun (1996) proposed a unifying framework known as the "fundamental triad", which combines the "match-mismatch" hypothesis of Cushing (1969) and the optimal environmental window hypothesis of Cury and Roy (1989). Bakun's (1996) fundamental triad explains how variability in fish stocks depends on the success of three processes: spawning, recruitment and retention. The 'ocean triad' processes (enrichment, concentration and retention) are likely to be influenced by environmental conditions (Bakun, 1998), influencing recruitment in fish species that produce

pelagic eggs during spawning ("match-mismatch" hypothesis) (Cushing, 1969). A number of studies (van der Lingen et al., 2001; Hutchings et al., 2002; Huggett et al., 2003; Petitgas et al., 2010) have supported these hypotheses. According to Bakun (1998), marine fish populations fluctuate on multiple time scales, caused by environmental forcing. Therefore, understanding the early life stages of individual fish species and observing how physics affects their recruitment success is important. One way of doing this is by comparing different species and ecosystems using a comparative approach (Bakun, 2010); this can give evidence of variability in the timing and intensity of spawning in the life cycles of small pelagic and demersal fish species that led to shifts in structure and functioning of coastal upwelling marine ecosystems (Cury and Roy, 1989).

Objectives and Research questions

This study is divided into two parts, firstly an analysis of patterns in the timing of spawning, and secondly an investigation into the environmental factors influencing recruitment of deep-water Cape hake. The main aim of the first part is to carry out a general synthesis of the timing and intensity of spawning of some important marine fish species found off South Africa and Norway. In addition, the study aimed to identify and understand short- and long-term variability in spawning seasons and to compare life cycles of fish species from the two regions. The second part of the study focuses on Cape hake species, particularly the deep-water Cape hake, creating spatial and temporal distribution maps of deep-water Cape hake juveniles over a period of ten years and describing the observed variability of these hake species on principal nursery grounds from 2003 – 2013. The influence of environmental variables on the abundance of deep-water Cape hake juveniles near the bottom will be assessed.

Two research questions are proposed for each part of the study. The key questions for the general synthesis study in Chapter 2 are as follows: (i) what are the patterns of timing and intensity of

spawning in fishes in the South African and Norwegian marine environments? (ii) what common environmental signals have been linked to short-term variability of life history events? For the second part of the study in Chapter 3, the key questions are: (i) does alongshore wind speed favour strong recruitment success of Cape hakes? (ii) do near-bottom oxygen concentrations influence selection of nursery grounds for deep-water Cape hake juveniles?

The dissertation is divided into four chapters. The introduction to the study is given in Chapter 1, providing context and background to Chapters 2 and 3. It also addresses the significance of the study and describes in detail the southern Benguela upwelling ecosystem as the main study site. Chapters 2 and 3 are laid out in a scientific paper style. Chapter 2 introduces the Norwegian high latitude marine environment and describes its physical dynamics as well as habitat preferences of its important fish species during the spawning season and their spawning periods. The data sources, analyses and approaches used to synthesize the result are described. The main results of this chapter are summaries of timings and durations of spawning events for fish species of two marine environments. Chapter 3 introduces the west coast nursery grounds of Cape hake species, produces spatial distribution maps, time series of recruitment and links between physical factors. Finally, Chapter 4 brings together the two previous chapters in the light of the key questions, and conclusions and recommendations are given for the study.

Chapter 2: Variability in the timing and duration of fish spawning off the coasts of Norway and South Africa

Abstract

Changes in oceanographic conditions in relation to life history events of fish have been evaluated by observing inter-annual variability using environmental and biological sampling and monitoring data since 1988. The purpose of this case study is to synthesize the patterns of spawning times and duration in life cycles of fish species found off Norway and South Africa, focusing on their short-term and long-term variability. Data collected from literature were used to identify the timing and intensity of spawning in fish life cycles in both regions using two manual approaches. Based on the temporal patterns of spawning times, it is shown that Norwegian fish species are strongly affected by seasonal environmental factors as they have confined and restricted spawning periods. This explains inter-annual differences observed previously, which are triggered by seasonal factors such as intensity of south-westerly winds (downwelling), light regime intensity and salinity stratification. Spawning times of South African fish species can vary depending on the availability of suitable habitat. These spawning times appear to be caused by intra-seasonal differences due to the strength of south-easterlies (upwelling), nutrient-limited waters and thermal stabilities.

Introduction

Intra-annual variability in life history events of fish species (particularly spawning) depends on the biophysical characteristics of the marine environment. Variability in spatial dynamics due to major physical and biological factors during spawning is not the only concern in research studies of fish life cycles but also variability in temporal dynamics. This is supported by previous studies (Shelton, 1987; Melo, 1994; Hutchings et al., 1998), which suggest that the locations in which fish species are found can influence the timing of spawning, depending on the biophysical variability of the ecosystem. Distinct types of intra-annual variability can influence low and high latitude marine environments in different ways, resulting in changes of the structure and functioning of the ecosystem for fish species to reach spawning success.

The southern Benguela, as a marine ecosystem in the low latitudes, experiences intra-seasonal variability both in physical and ecological dynamics. Strong "pulses" of upwelling last approximately 12 days, during a six-month period (Hutchings et al., 1995). These upwelling events result in 'blooms' of phytoplankton during this six month period (Pitcher and Weeks, 2006). Wind forcing and the presence of phytoplankton and zooplankton is important during the early life history events of fish in the southern Benguela, as most of the productivity dynamics are on intra-seasonal scales (Hutchings et al., 1995). The seasonal changes in wind forcing have an influence on hydrographical conditions and nutrient availability in the southern Benguela (Pitcher, 1992). Thermal stabilization of the water column in early spring over the Agulhas Bank and offshore on the west coast, after deep mixing during winter months (Shannon et al., 1984), results in a weak intensity of local phytoplankton blooms.

The main zooplankton prey species of the dominant pelagic fish species in the southern Benguela are copepods such as *Calanoides carinatus* and *Calanus agulhensis* (Pitcher, 1992). These prey

species are closely associated with the seasonality of upwelling events and phytoplankton blooms (Verheye et al., 1992). The peak periods of copepod abundance differ along the coast of the southern Benguela with monthly variability driven by top-down effects (Verheye et al., 1992). Zooplankton populations peak in the southern Benguela during late autumn and spring on the western Agulhas Bank, while in St. Helena Bay the peak is in late summer (Verheye et al., 1992). High biomass of phytoplankton and an increase in zooplankton abundance favours the production and consumption cycle of fish species to successively spawn for prolonged periods in the southern Benguela (Shannon et al., 2006).

The high latitude marine environment of Norway experiences inter-annual variability influenced by ecological and physical dynamics. The Norwegian Sea is located in the North Atlantic Ocean, northwest of Norway, and is bounded by the North Sea, the Greenland Sea, the Barents Sea and the North Atlantic Ocean (Figure 2.1). The warm North Atlantic Current, an extension of the Gulf Stream, transports heat from the North Atlantic Ocean, bringing warm, saline water onto the Norwegian central shelf (Loeng and Drinkwater, 2007) and providing Norway with ice-free harbours throughout the year (Sætre and Ljoen, 1972). Norwegian shelf water is cooled by the overflow of Arctic water (Sætre, 1999). Norwegian coastal water is fed by freshwater run-off from the southern part of Norway (North Sea) and North Atlantic Drift Water (Hansen et al., 2001). These waters mix on the central Norwegian shelf, contributing to the formation of the Norwegian Coastal Current (NCC) (Sætre and Ljoen, 1972). The cyclonic circulation on the Norwegian central shelf is characterised by the Norwegian Coastal Current flowing in a north-easterly direction along the Atlantic coast of Norway to the Barents Sea (Sætre, 1999). It is separate from the North Atlantic Current (NAC) (Figure 2.1), transporting colder and less saline water than the NAC, most of which comes from the Norwegian fjords (Loeng and Drinkwater, 2007). The

Norwegian Coastal Current splits into two branches; the minor part follows the continental shelf then disappears and the major one partly contributes to a coastal jet (Sætre, 1999). The Norwegian Coastal Current is both wind-driven, with water upwelling along the Norwegian coast through the action of south-westerly winds creating pressure gradients, and also driven by its salinity distributions which, in turn, create density gradients that contribute to downwelling (Sætre and Ljoen, 1972). The several coastal banks on the Norwegian central shelf induce anticyclonic topographically trapped eddies (Sætre, 1999), influencing fish population dynamics.

Ecosystems of the Barents Sea, Norwegian Sea and North Sea (Figure 2.1) interconnect ecologically although they are isolated from each other. The Barents Sea has a relatively shallow shelf and its oceanographic conditions are strongly affected by transport from the Norwegian Sea (Loeng and Drinkwater, 2007). The Barents Sea contains one of the most productive ecosystems in the world, owing to inflow of warm currents from the North Atlantic and upwelling of nutrient rich waters (Loeng and Drinkwater, 2007). The two most important ecosystems for early life stages of many targeted fish species in the Norwegian region are the Norwegian Sea ecosystem and the Barents Sea ecosystem (Hislop, 1984).

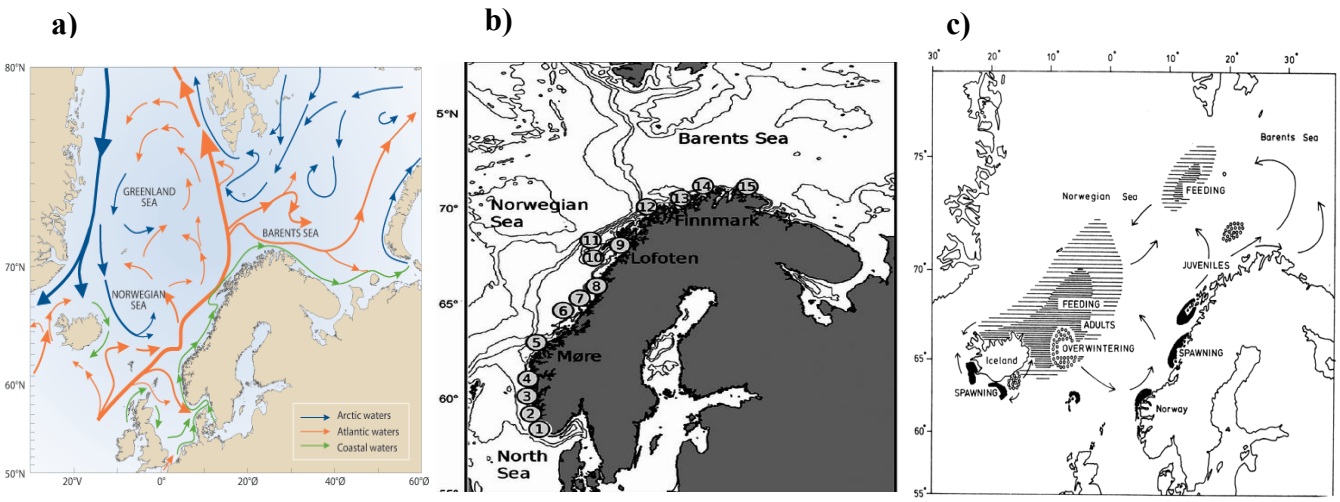

Figure 2.1: Maps showing (a) the circulation around Norway and surroundings, (b) three Norwegian ecosystems and (c) suitable habitats for life history events of fish life cycles (extracted from Sætre, 1999; Olsen et al., 2010).

The seasonal variability of the production cycle in Norwegian ecosystems is predominantly determined by the availability of light and the strength of the wind stress (Longhurst, 1995). In spring and summer, Norwegian ecosystems experience predominantly south-westerly winds, which play a role in pelagic production and consumption (Longhurst 1995). Seasonality in the Norwegian Sea ecosystem is not uniform and the strong winter mixing is restricted by salinity stratification between July and August (summer) (Longhurst, 1995). The main process of primary production begins in early March through April, when there are usually enhanced nutrients and high levels of light (Broms and Melle 2007). In early May, the spring bloom develops as stratification increases, appearing in coastal waters over the Norwegian shelf (Longhurst, 1995). During summer, there is a decrease in primary production, which is then supported mainly by regenerated nutrients (Prokopchuk and Sentyabov, 2006). In winter and early spring, phytoplankton standing stock is reduced and during autumn there is wind mixing and a small phytoplankton bloom is generated. Although there are plenty of nutrients in October,

phytoplankton productivity usually declines during this period because of limitations in light levels (Prokopchuk and Sentyabov, 2006). Variation in the timing of the 'spring bloom' is related to seasonality among water masses (Broms and Melle, 2007).

The seasonality of the zooplankton production cycle is closely linked to spring bloom formation in Norwegian ecosystems (Melle et al., 2004). Hence, the Norwegian Sea is the main feeding area for pelagic fish stocks in the north-east Atlantic region (Holst and Iversen, 1992). *Calanus finmarchicus* is one of the main prey species exerting "bottom-up" trophic ecosystem controls in the Norwegian and Barents Seas. It overwinters in the deep Norwegian Sea (Prokopchuk and Sentyabov, 2006). It ascends to the upper mixed layer in spring and is transported by Atlantic inflow to the Barents Sea (Prokopchuk and Sentyabov, 2006) where it is the main food source for most commercially valuable fish species of Norway. High zooplankton productivity during summer enhances feeding migration of Norwegian pelagic fish (Hamre, 1990). *Calanus finmarchicus* is a crucial prey species that pelagic fish like herring rely on for the build-up of depleted fat reserves after they spawn early in spring (Prokopchuk and Sentyabov, 2006).

The Norwegian Sea ecosystem is a habitat suitable for spawning of Norwegian fish species as it has several coastal banks, while the Barents Sea ecosystem is used by Norwegian fish species during juvenile stages as it acts as a nursery ground (Olsen et al., 2010). Habitats in Norwegian waters suitable for spawning are outside the Lofoten area, Møre area and Finnmark fjords (Figure 2.1b). Species assemblages are defined by the preference for certain environmental conditions. The species richness in Norwegian habitats is enhanced on the coastal banks (at depths of 50 – 100 m) for pelagic fish assemblages and (at depths of 300 – 600 m) for deep-sea fish assemblages (Bergstad et al., 1987). The overlap in distributions of common abundant fishes found off Norway, such as capelin (*Mallotus villosus*) and Norwegian spring-spawning herring (*Clupea harengus L.),*

is clear during their spawning migrations, when they appear in dense schools (Olsen, 2010). Similar observations have been made for haddock (*Mellanogrammus aeglefinus*) and Arcto-Nowergian cod (*Gadus morhua*), with the schools following the main Atlantic inflow water masses at depths over 200 m for the spawning migration (Olsen, 2010).

The Norwegian Coastal Current is an important transport route, carrying fish eggs and larvae from the spawning areas northwards to nursery areas along the coast and to the Barents Sea (Ellertsen et al., 1989). The Barents Sea has abundant marine fish stocks that are important ecologically, including pelagic fish species such as capelin and Norwegian spring-spawning herring. Capelin is a key species in this ecosystem, undergoing large fluctuations due to recruitment failure (Olsen et al., 2010). Norwegian cod is the most abundant demersal fish species found in this ecosystem, but its abundance and distribution fluctuate rapidly due to variability in the oceanographic conditions of Norwegian waters (Hislop, 1984). Migration routes of these fish species for returning to spawning grounds vary throughout the year and inter-annually (Kaartvedt, 2000).

The most socio-economically valuable fish species in Norway are a small pelagic fish species (Norwegian spring-spawning herring) and a demersal fish species (Arcto-Norwegian cod). Norwegian spring-spawning herring mainly spawn off the Norwegian coast during spring then migrate westwards into the Norwegian Sea in search of food (Olsen et al., 2010). Arcto-Norwegian cod are the Atlantic cod inhabiting the coastal spawning banks of Norway. Arcto-Norwegian cod is the main demersal species targeted by fisheries in Norwegian waters (Brander, 2005). This demersal fish stock mostly co-occurs with pelagic fish during spawning and hatching and is associated with Atlantic water masses of the Barents Sea and Norwegian coast (Sundby and Nakken, 2008). Cod are multiple batch spawners, with most stocks spawning between February

and May (winter and spring), although some stocks spawn as early as January and some as late as August (Ottera˚ et al., 2006).

The spawning period for cod in the fjords of western Norway coincides with frequent winds from the south, and consequently down-welling (Brander, 2005). Spawned eggs of cod are typically found in upper surface waters (Brander, 2005). The eggs take ten to thirty days to hatch depending on temperature (Otterå et al., 2006). Spawning duration can be influenced by temperature variability in Norwegian ecosystems. Extremely cold temperatures typically result in delayed spawning through slow gonad development (Brander, 2005). In contrast, warm temperatures favour early gonad development, resulting in earlier spawning. Ellertsen et al. (1989) discovered that the relationship between temperature at the spawning site and spawning time of cod depends on local hydrography and fish distribution. Most fish species tend to prefer specific temperature ranges (Ellertsen et al., 1989). Long-term changes in temperature, which might be marked, could lead to expansion or contraction of fish distributions (Sims et al., 2004). Species with restricted spawning seasons, such as in the Norwegian ecosystems, tend to produce offspring with a relatively narrow range of birthdates (i.e. hatch dates), which create greater potential to be impacted by environmental factors (Otterå et al., 2006). Most pelagic fish species in Norwegian waters begin their spawning during the beginning of seasonal stratification in April and May (spring) and at this point there is usually an increase in surface water temperature above 14^0C and eggs are generally found in the surface layer (<15m-depth) (Otterå et al., 2006). Strong seasonal changes in the physical environment of Norwegian ecosystems can trigger spawning and lead to inter-annual differences in spawning times (Otterå et al., 2006).

The differences in oceanographic features between Norwegian high latitude marine environments and the southern Benguela low latitude environment are complex. Major physical features such as

the Norwegian coastal current, density stratification and strong seasonality in spawning in relation to the primary production cycle occur in the Norwegian region. In contrast, the southern Benguela is highly dynamic, depending mostly on the strength of upwelling, which can influence spawning success by the intra-seasonal variability in environmental dynamics. The southern Benguela has closely linked habitats supporting life history events of fish life cycles. Ecosystems off Norway that play a role in these key events comprise three regions distant from one another. There are also similarities between Norway and the southern Benguela; both of their coastal currents are wind-driven and, although the Norwegian ecosystems are isolated, the habitats they interconnect in terms of fish population dynamics are similar to habitats of the southern Benguela.

This desktop study aims to give a focused review of the timing of spawning and spawning duration of a few selected fish species found off South Africa and Norway. The fish species are selected because of their commercial and ecological importance in their ecosystems. Knowledge about environmental factors driving spatial distributions of these fish species has been widely documented. However, there is limited information regarding temporal variability at intra-annual scales for some fishes' life cycles. The main focus will be to analyse short-term and long-term changes in spawning seasons and to compare patterns of fish spawning duration from both regions.

Methods: Data sources and analysis

A comparison of spawning times and spawning duration for small pelagic and demersal fish species found off southern Africa and Norway was carried out using a qualitative manual analysis approach. The geographic areas covered latitude and longitude ranges extending from 28ºS – 35ºS and from 18ºE – 22 ºE off South Africa and from 55ºN – 70ºN and 25ºE – 50 ºE off Norway. The coastal pelagic fish species selected for the southern Benguela region were anchovy (*Engraulis encrasicolus*), sardine (*Sardinops sagax*), round herring (*Etrumeus whiteheadi*) and Cape horse mackerel (*Trachurus capensis*), while the demersal fish were both Cape hakes (shallow-water Cape hake (*Merluccius capensis*) and deep-water Cape hake (*Merluccius paradoxus).* In the Norwegian region, the selected small pelagic fish species was the Norwegian spring-spawning herring (*Clupea harengus L.*) and the demersal fish species was the Arcto-Norwegian cod (*Gadus morhua*). Spawning data were considered from 1980 to 2015.

Local movements of mature fish to spawning grounds were considered spawning migrations. Short-term variability in spawning migration periods of these species was analyzed. Other abundant fish species found off the coast of Norway, such as capelin (*Mallotus villous)*, saithe (*Pollachius virens),* north-east mackerel (*Scomber scombrus)* and haddock (*Melanogrammus aeglefinus),* were also considered in the analysis of spawning migration times. Short-term variability in spawning migration periods were compared in both study regions.

Life history data were obtained via internet search (Google scholar) and journal databases (ScienceDirect, Springer, UCT thesis databases in the library catalogue and the databases from Institute of Marine Research, Bergen, Norway). Information was taken from theses, conference papers, reports, journal articles and websites of marine fisheries organizations. Findings and results of each study reviewed were assessed using two manual approaches: systematic and meta-

analytical. The systematic approach was used to synthesize harvested information, where the findings of previous work about the environmental factors influencing spawning migration were accumulated and compared, creating a broad overview of existing studies. For the meta-analysis, the timing and intensity of spawning events in life cycles of different fish species were assessed. This comparative approach helped identify distinct patterns of spawning from 1980 – 2015.

The types of data used to identify spawning are listed in Table 2.1 along with the methods used in the previous studies to obtain the spawning estimates. Sampling tools were categorized into two forms: gonadosomatic indices and egg surveys indicated in orange on figures.

Table 2.1: Sources of information and their data products and methods to assess spawning estimates of selected fish species off South Africa and Norway

South Africa and Norway fish species	Sampling tools to obtain data in the sources	Data to identify spawning estimates	Sources
Anchovy *(Engraulis encrasicolus)*	Annual Calvet net surveys Annual November biomas surveys Annual hydro-acoustic surveys Annual ichthyoplankton surveys Monthly SARP surveys Egg production method	Egg abundance Spawning biomass Catch per unit effort Egg density Oocyte volume Egg concentration	Van der Lingen et al. (2001), Hampton (1996), Shelton and Hutchings (1982), Shannon et al. (1996), Mullon et al. (2003), Parada et al. (2008), Barange et al. (2009) Huggett et al. (2003), Hutchings et al. (1998), Coetzee et al. (2008)
Sardine *(Sardinops sagax)*	Annual Calvet net surveys Annual acoustic surveys Annual ichthyoplankton surveys Annual November biomass surveys Egg production method	Egg abundance Catch per unit effort Egg density Oocyte volume Spawning biomass Egg concentration	Huggett et al. (1998), Armstrong et al. (1988), Hutchings et al. (1998), Shelton and Hutchings (1982)
Round herring *(Etrumeus whiteheadi)*	Annual pelagic acoustic surveys Monthly egg surveys Annual ichthyoplankton surveys CELP surveys	Catch per unit effort Egg density Oocyte volume	Roel (1990), Roel and Armstrong (1991) Roel and Melo (1990), Amstrong et al. (1991), Crawford (1980), Hampton (1996), Shelton (1987),
Cape horse mackerel (*Trachurus capensis*)	Annual Calvet net surveys Monthly Inshore surveys Annual ichthyoplankton surveys	Catch per unit effort Oocyte volume Egg density	Hecht (1990), Barange (1998),Geist (2014), Ndjaula et al. (2013)
Deep-water Cape hake *(Merluccius paradoxus)*	Annual Nansen surveys Monthly inshore/longline/handline surveys	Catch per unit effort Spawning biomass	Strømme and Lipinski (2015), Miller et al. (2006), Garavelli et al. (2012), Grote et al. (2007), Grote et al. (2012),
Shallow-water Cape hake *(Merluccius capensis)*	Annual Nansen surveys Inshore/longline/handline surveys	Catch per unit effort Oocyte volume Egg abundance	Strømme and Lipinski (2015), Jansen et al. (2015) Miller et al. (2006) Le Clus 2005b
Norwegian spring-spawning herring (*Clupea harengus L.)*	Annual hydro-acoustic surveys Annual pair trawl surveys Monthly egg surveys Egg production method	Spawning stock biomass Catch per unit effort Gonad weight Egg density	Slotte and Fiksen (2000), Hamre (1990) Dragesund et al. (1997), Rottingen (1992), Slotte et al. (2000), Sinclair et al. (1984)
Arcto-Norwegian cod *(Gadus morhua)*	Annual hydro-acoustic surveys Annual trawl surveys Monthly egg surveys Egg production method	Spawning stock biomass Catch per unit effort Egg abundance Gonad weight	Huse and Ona (1996), Rottingen (1992), Hansen et al. (2001), Sundby and Nakken (2004), Sundby (2008), Pedersen (1984), Brander (2005)

Results

In general, commercially valuable fish species in the southern Benguela spawn seasonally or year round (Figure 2.2). Schooling fishes remain in the pelagic habitat throughout their spawning period whereas demersal fishes have pelagic egg and larval stages. Anchovy spawn in late spring and summer (October – February). Sardine spawn throughout the year, with spawning peaks between October and December. Round herring spawn in late winter and early spring (June/July to September/November). Cape horse mackerel spawning period is mostly in spring and summer but also during winter. Shallow-water Cape hake spawn between September and February, with a spawning peak in late summer, whereas deep-water Cape hake show extended spawning throughout the year with two main spawning peak periods from September to November and February to March.

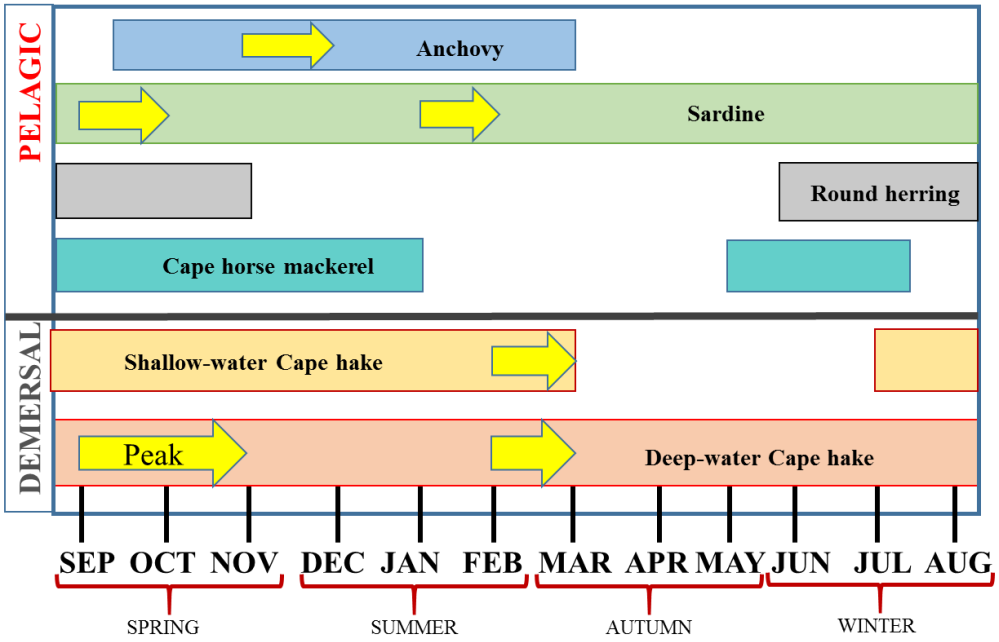

Figure 2.2: Schematic representation of typical spawning times and peak duration (yellow arrow) for shallow-water Cape hake, deep-water Cape hake, round herring, sardine, Cape horse mackerel and anchovy in the southern Benguela upwelling ecosystem. (Findings extracted from Hutchings et al., 2002).

Unlike the targeted fishes of the southern Benguela, the two important commercial fish species in Norway have concise and restricted spawning times (Figure 2.3). Norwegian spring-spawning herring spawn between February and April in the pelagic zone. Arcto-Norwegian cod (Sundby and Nakken, 2008) spawn between March and May

in the demersal habitat. Cod eggs are vertically distributed in the pelagic zone in late spring. From late summer to winter, these Norwegian fish species rarely spawn.

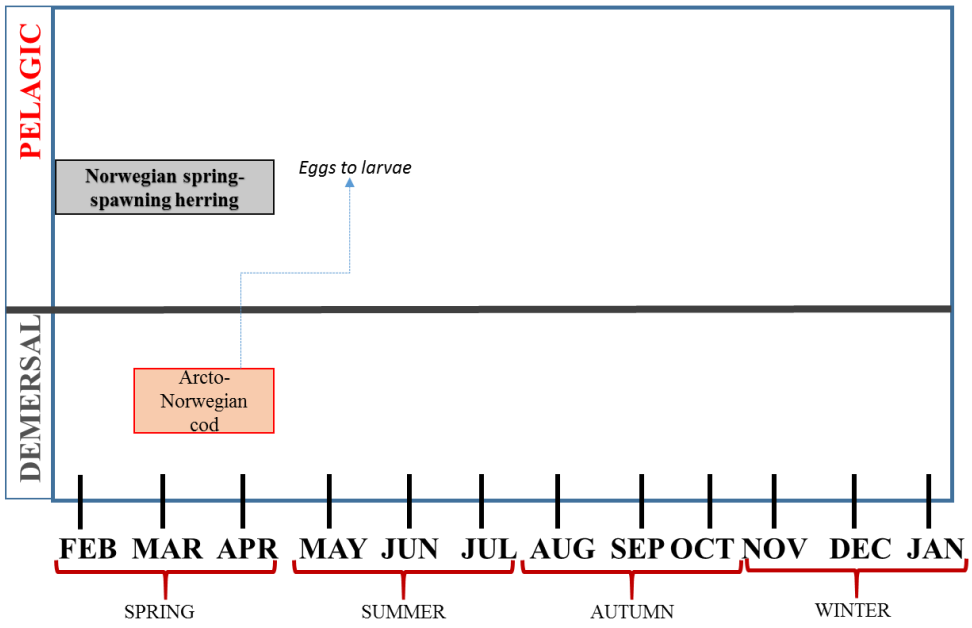

Figure 2.3: Schematic representation of typical spawning times and vertical distribution of spawning (eggs and larvae) for two important commercial species off Norway (Arcto-Norwegian cod and Norwegian spring-spawning herring). (Findings redrawn from Olsen et al. 2010).

The duration of migration prior to spawning by fishes of these regions is completely distinct (Table 2.2). Migration to spawning grounds occurs within a single season for fish species found in the southern Benguela. For most species of the southern Benguela, the spawning migration period is during summer except for deep-water Cape hake where it occurs during spring. Fish species off Norway show expanded migration periods occurring in more than one season. There are similarities in potential influences of spawning migration duration in the southern Benguela and Norway. Similar environmental conditions that possibly influence spawning migration durations in the two regions are winds, although Norwegian upwelling-favourable winds are south-westerly whereas in the southern Benguela they are south-easterly.

Table 2.2: Duration of spawning migration in the life cycles of demersal (pink) and pelagic (orange) fish species found off the Southern Benguela and Norway, including possible environmental conditions influencing the duration of spawning migrations.

South Africa and Norwegian fish species (demersal –pelagic)	Spawning migration period	Possible influence of environmental conditions	Comments	Sources
Shallow-water Cape hake (*Merluccius capensis)*	January-February (summer)	Thermal stabilities unfavourable winds low oxygenated waters	Short migration period	Jansen et al. (2015);Grote et al. (2007), Grote et al. (2012)
Deep-water Cape hake (*Merluccius paradoxus*)	November-December (spring)	Thermal stratification unfavourable winds low oxygenated waters	Short migration period	Stenevik et al. (2008); Garavelli et al. (2012), Grote et al. (2012)
Anchovy (*Engraulis encrasicolus)*	January-February (summer)	Thermal stabilities Unfavourable winds Nutrient-limitation	Short migration period	Huggett et al. (2003); van der Lingen et al. (2001)
Round herring (*Etrumeus whiteheadi*)	January-February (summer)	Thermal stabilities Unfavourable winds Nutrient-limitation	Short migration period	Roel (1990), Roel and Armstrong (1991)Roel and Melo (1990),
Sardine (*Sardinops sagax)*	January-February (summer)	Thermal stabilities Unfavourable winds Nutrient-limitation	Short migration time	Coetzee and van der Lingen (2008); Beckely and van der Lingen (1999)
Horse mackerel (*Trachurus capensis*)	January-February (summer)	Thermal stabilities Unfavourable winds Nutrient-limitation	Short migration time	Hecht (1990) Kerstan and Leslie (1994) Laverty (2012)
Arcto-Norwegian cod (*Gadus morhua*)	August-January (late summer-winter)	Salinity stratification South-westerly winds downwelling	Long migration time	Bergstad et al. (1987), Sundby and Nakken (2008),Olsen et al. (2010)
Haddock (*Melanogrammus aeglefinus*)	July-January (summer-winter)	Salinity stratification South-westerly winds	Long migration time	Bergstad et al. (1987),Olsen et al. (2010)
Saithe (*Pollachius virens*)	June-January (summer-winter)	Salinity stratification South-westerly winds	Long migration time	Hollowed and Sundby 2014,Olsen et al. (2010)
NSS herring (*Clupea harengus L.*)	April-June October-January (spring-winter)	Salinity stratification South-westerly winds Weak upwelling	Long migration time	Slotte et al (2000),Olsen et al. (2010), Holst et al. (2002) Skagseth et al. (2015)
Capelin (*Mallotus villosus*)	May-February (summer-winter)	Salinity stratification South-westerly winds	Long migration time	Rottingen et al. (1990),Olsen et al. (2010)
NE Atlantic mackerel (*Scomber scombrus*)	May-July (summer)	Salinity stratification South-westerly winds	Short migration time	Holst and Iversen, (1992)

Comparison of spawning of fish species in the southern Benguela and Norway

The dominant methods used to obtain the spawning times in Figure 2.4 and 2.5 are from egg surveys, hydro-acoustic surveys or icthyoplankton surveys. Other methods were the egg production method to investigate egg maturity and fecundity as well as examination of specimens to derive gonado-somatic indices.

There has been temporal variability in spawning of anchovy and sardine in the southern Benguela (Figure 2.4a and b). The spawning peak of anchovy is typically during November, when eggs and adults are found on the Agulhas Bank spawning grounds. In the 1980s and 1990s spawning had long duration, as it began in September until February/March. However, from 2001 until recently the spawning period seems to have ended early in December/ January, also associated with spawning peaks in both November and December. In the early 1990s there was a shift in spawning period, beginning in October, not September, and ending in March in 1990 –, 1992 and 1994. These data exclude anchovy spawning periods for 2000, 2011 and 2013 – 2015, as there were no literature data found for these years. For 1991, 2003 and 2008, there is evidence of spawning peaks in February, September and March.

Similar to patterns in anchovy spawning times, sardine have varied their spawning (Figure 2.4b). However, there are no shifts in historical years (1980s and 1990s); the spawning durations are consistent. There was little information from the 1980s and 1990s about the intensity of sardine spawning. Years that are more recent indicate that sardine spawning peaks in September – October and February – March. Weak spawning was noted in April of 1995, 1998, 1999, 2009 and 2011. In 2002, 2003, 2005, 2009 and 2012 spawning is observed to begin earlier than expected, in August. Spawning occurred all year round in 1998 and 1999.

There is no temporal variability observed in the spawning period of round herring (Figure 2.4c), but there is some variability in the intensity of spawning. All years for which data were available indicated that spawning is throughout the year and has not changed. However, the spawning intensity had slight changes in 1983, 1987, 1993 and 2001 – 2002, indicating weak spawning during summer and early autumn (November – April), whereas in 1993 weak spawning occurs from August – September. The strong spawning peaks from May – July appear to be consistent in most years in the 1980s, late 1990s and early 2000s.

Cape horse mackerel spawning times and intensity are not well understood, and spawning is noted in most seasons (Figure 2.4d). There is a slight shift from 1994 until 2011; this excludes the years for which there were no data. In the late 1980s, 1990s and recent years, Cape horse mackerel appears to have spawned twice a year, from September to January and May to August. This is different from the evidence in 2013 – 2015 studies, where horse mackerel spawned from December to July and September to April, with greatest spawning intensity between summer and autumn. The strong intensity of spawning during March and April is not supported by the findings of most years, but was observed in 1983 – 1985.

The spawning times and intensity of demersal trawl species indicate that shallow-water Cape hake spawning times are distinct from those of deep-water Cape hake. Shallow-water Cape hake is observed to mostly spawn from September to March (Figure 2.4e). Spawning times for shallow-water Cape hake in the 1980s, 1990s and early 2000s were different from those in the late 2000s. The deep-water Cape hake spawning period remains consistent from historical years to recent years, with deep-water Cape hake spawning all year round (Figure 2.4f). Spawning intensity seems to have increased for both species in recent years. Shallow-water Cape hake show reduced spawning intensity in 1986 and 1999, whereas deep-water Cape hake show two spawning peaks,

one strong and one weak, for some years (1983, 1986, 1995, 2001, 2003, 2008, and 2013) and no evidence of a secondary peak in other years. Weak spawning in 2008 and 2013 occurred in February/March. Recent years show evidence of expansion of spawning intensity, from August to October in 2005, 2007, 2008, 2012 and 2015. For shallow-water Cape hake, evidence of extended spawning is noted for 2007, 2011 and 2012, from July to October. In the 1980s, the strongest intensity of spawning started in November/December.

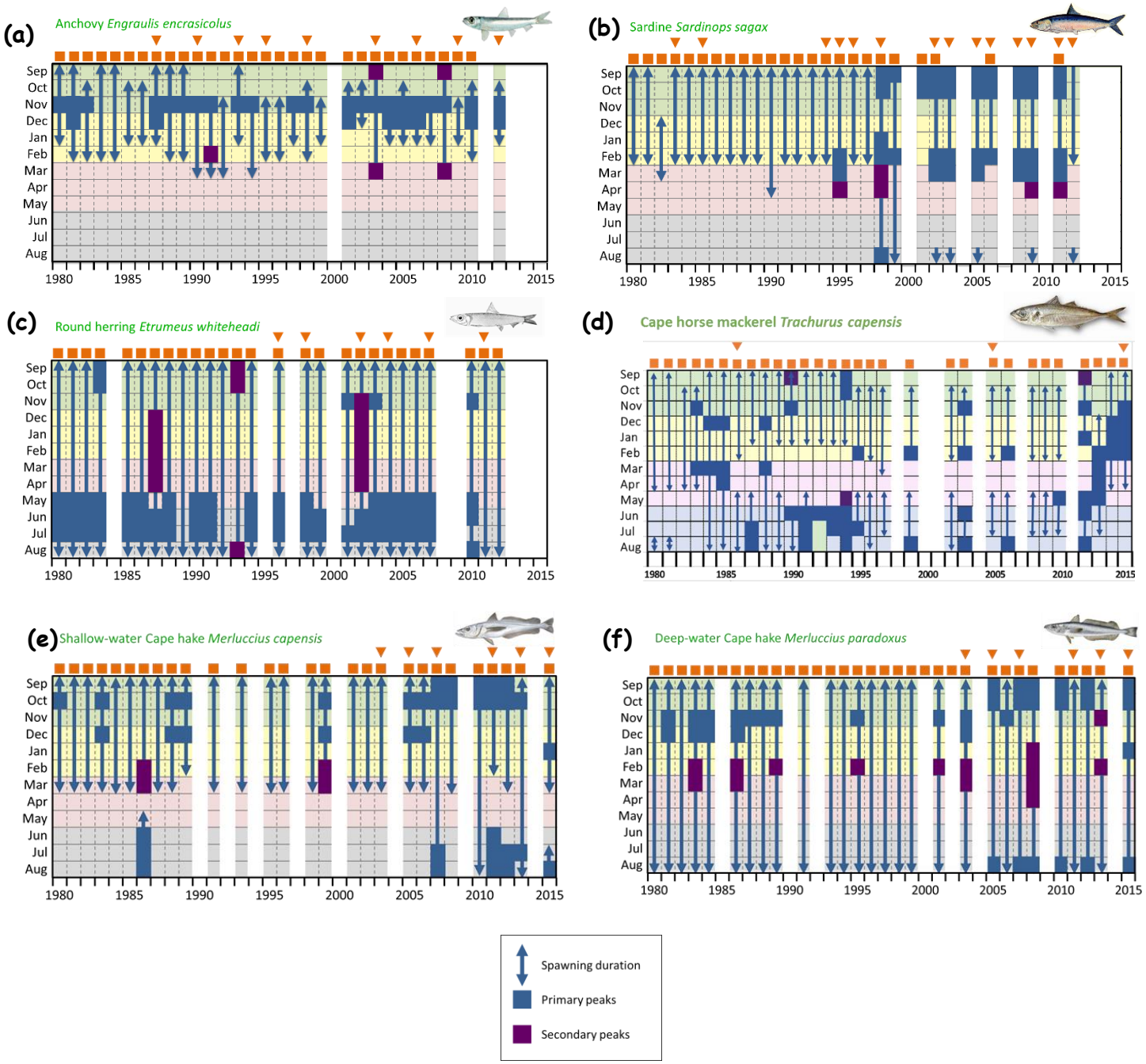

Figure 2.4: Synthesis of spawning periods and spawning intensity in the southern Benguela from 1980-2015 for (a) anchovy (*Engraulis encrasicolus*) and (b) sardine (*Sardinops sagax*) (c) round herring (*Etrumeus whiteheadi*) and (d) Cape horse mackerel (*Trachurus capensis*) (e) shallow-water hake (*Merluccius capensis)* and (f) deep-water hake (*Merluccius paradoxus*). Orange symbols are referring to the kinds of data products for spawning estimates.

There is less temporal variation in spawning of the two important commercial fish species found off Norway (Figure 2.5a and b) than noted for the southern Benguela. The spawning times of Norwegian spring-spawning herring (Figure 2.5a) have not changed from the 1980s and early 1990s. Spawning occurs from February – April (spring). There were some changes from the late 1990s, when spawning times shifted from March to May. Norwegian spring-spawning herring spawning intensity is strong in early years of the 1980s and 2000s, showing peaks during March/April. There was weak spawning in 2000 and 2006.

The spawning times of arcto-Norwegian cod (Figure 2.5b) are consistent in the early 1980s and 1990s. There was a change in the late 1990s and recent years, similar to the Norwegian spring-spawning herring. Strong spawning intensity of cod is only found in the 1980s, and not in the early 2000s, as in Norwegian spring-spawning herring. Consistent spawning peaks are during April in the early 1980s and in March and April in the early 1990s and early 2000s. Similar to the Norwegian spring-spawning herring, there were weak spawning peaks in May 2002 and 2004. The spawning duration of cod remained consistent in most years, similar to the deep-water Cape hake.

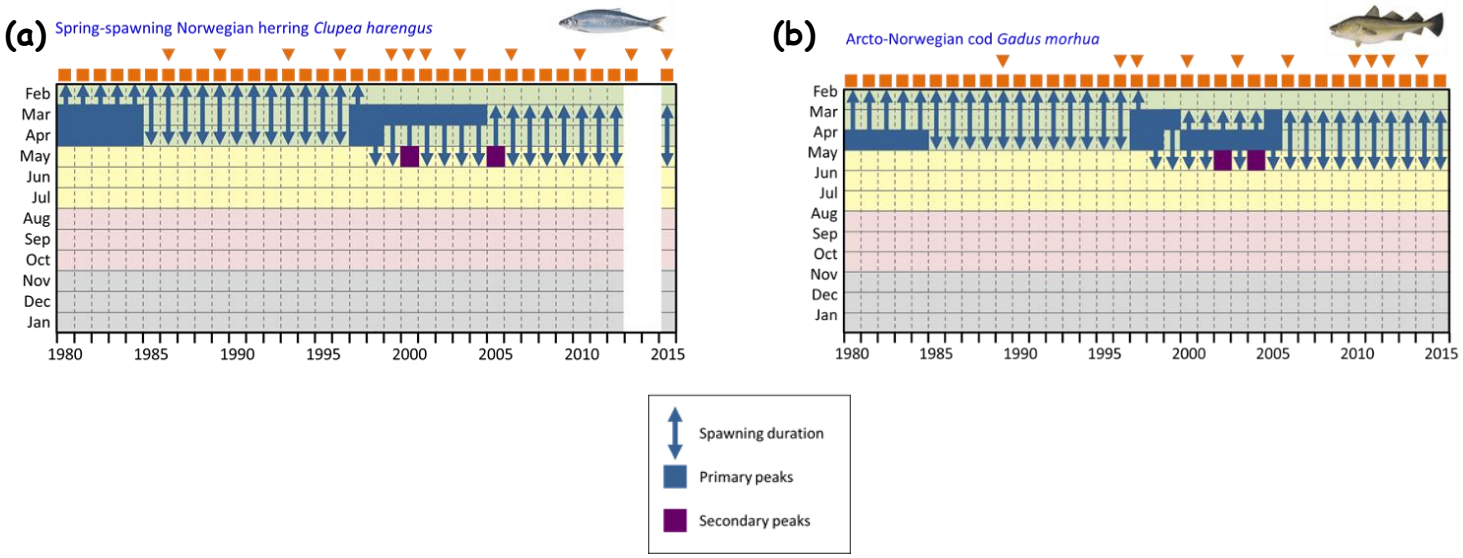

Figure 2.5: Synthesis of spawning periods and spawning intensity in high latitude marine environments off Norway from 1980-2015 for (a) Norwegian spring-spawning herring (*Clupea harengus L.)* and (b) Arcto-Norwegian (*Gadus morhua*). Orange symbols are referring to the kinds of data products for spawning estimates.

Discussion

Difference between fish species off southern Benguela and Norway

Spawning time and duration is more variable in small pelagic fish of the southern Benguela than of Norway. Le Clus (1990) suggested that the difference in spawning times of anchovy is mostly affected by sea surface temperature (SST) anomalies, which is different from that of sardine that is affected by currents enhanced by south-easterly winds. There was a consistent spawning peak in November for anchovy during the 1980s and 1990s. However, surveys were mostly carried out in November/December conducted during those years, which could bias the results. Historical studies (Armstrong et al., 1982; Olivar et al., 1988; Bloomer et al., 1994) have suggested that in November anchovy spawn intensively. Sardine, on the other hand, do not have consistent peak spawning times. Double spawning peaks of sardine were observed in the late 1990s compared to anchovy. This is not surprising since spawning intensity can be influenced by the location at which spawning occurs, as sardine eggs are found throughout the southern African region (Fowler 1998). This might imply that sardine spawning is non-selective in environmental conditions, as long as they are on spawning grounds. Indeed, Twatwa et al. (2005) suggested that the sardine spawning strategy is flexible and is capable of taking advantage of wide ranges of environmental variables. Shifts in spawning times were noted in most small pelagic fishes, especially in the late 1990s and early 2000s (Figure 2.4). Previous studies (Le Clus, 1990; van der Lingen et al., 2006; Roy et al., 2007) that address shifts in spawning explain anchovy shifts by environmental conditions, spawning location and period, but there is little information on spawning shifts of other small pelagic fishes in the southern Benguela.

In contrast to the extended spawning times of anchovy and sardine, Norwegian spring-spawning herring spawn over a 3-month period. This small pelagic fish species is a determinate, one-batch

spawner (Slotte et al., 2000). The sudden change in the spawning period from 1998 was probably influenced by environmental anomalies. Skagseth et al. (2015) explained that extremely cold temperatures and an increase in density structure resulted in downwelling. This influenced egg and larval survival of Norwegian spring-spawning herring at the bottom on the spawning grounds along the Norwegian coast as they are brought into the pelagic zone.

It is clear that spawning peaks of small pelagic fishes in this case study vary. Peruvian anchovy (*Engraulis ringens*), which inhabit another eastern boundary upwelling system (Humboldt upwelling ecosystem) off South America, spawn sporadically throughout the year with a peak in spring (August to October) and a secondary peak in summer (January – February) (Alheit et al., 1984). Unlike the Norwegian spring-spawning herring, Pacific herring (*Clupea harengus pallasi*) (Hay, 1985) spawn in varying seasons because of unsuitable environmental conditions, which influence the timing of spawning. This Pacific small pelagic fish species is mostly a winter-spring spawner (Hay, 1985). This indicates that spawning duration is extended, not like the restricted spawning duration of Norwegian spring-spawning herring. Northeast Atlantic sardine (*Sardina pilchardus*) (Petitgas et al., 2010) off Portugal have two spawning peaks, one in winter (November – January) and the other in summer (April – May), different to the southern African sardine as its peaks are mostly during spring (Figure 2.2).

Cape hakes in the southern Benguela region show evidence of consistent spawning times in most years. Despite this evidence, in most of the recent years in Figure 2.4e and f, Cape hakes' spawning times and intensity shows interchanging patterns. The distinct spawning duration of these demersal fish species has been explained by various historical studies (Botha, 1986; Olivar et al., 1988; Payne et al., 1989; Payne and Punt, 1995) and recent studies (Sundby et al., 2001; Burmeister, 2005; Stenevik et al., 2008; Grote et al., 2012 Jansen et al., 2015; Strømme et al., 2015). The weak

spawning intensity of Cape hakes in Botha's (1986) findings were associated with the main upwelling season. However, the recent study of Strømme et al., 2015 showed that there is no secondary spawning of Cape hakes in the southern Benguela.

The consistent spawning times noted in historical years for shallow-water Cape hake disappeared in recent years and the spawning durations were expanded, starting earlier than before (Figure 2.4a). The main spawning period of shallow-water Cape hake appears to be summer; the spawning peaks largely coincide with peaks of phytoplankton production (Jansen et al., 2015). However, Kainge et al. (2007) found that spawning times of shallow-water Cape hake is throughout the year with spawning peaks between July and October.

The spawning times of deep-water Cape hake are year-round, with increased intensity around March, August and October. A single spawning peak of deep-water Cape hake, as suggested by Botha (1986), contrasts with recent studies (Grote et al., 2007; Grote et al., 2012; Strømme et al., 2015), where increased spawning occurs during periods of weak upwelling intensity. Studies are still underway to determine if these fish stocks, especially deep-water Cape hake, are single or shared stocks of Namibia and South Africa. Jansen et al. (2015) and Burmeister (2005) show multiple spawning peaks and locations for both Cape hake species, strongly supporting the hypothesis of multiple stocks according to reproduction units.

Difference between regions (pelagic and demersal fish)

It is evident that southern Benguela fish species have variable spawning duration and peaks, unlike Norwegian fish species, which have spawning periods that are limited and restricted on an intra-annual scale. The temporal pattern of spawning observed between these regions suggests that the environmental dynamics influencing spawning habitats are different. Longhurst (1995) explained

that the seasonality in the Norwegian Sea ecosystem is not uniform and the strong winter mixing is restricted by salinity stratification between July and August (summer). There was a bi-seasonal cycle observed in recent years in the spawning peaks of fish species found off the southern Benguela (Figure 2.2), where most of these species (anchovy, sardine, round herring, horse mackerel, shallow-water Cape hake and deep-water Cape hake) were observed to have double spawning peaks occurring in different seasons. In contrast, Norwegian fish species (Norwegian spring-spawning herring and Arcto-Norwegian cod) had uniform spawning peaks. This indicates that most of these southern Benguela fish species are able to find suitable environmental conditions during spawning times, or they can tolerate a broad range of physical dynamics during the spawning period, which results in weak spawning peaks. This supports the findings of Fowler (1998) and van der Lingen and Huggett (2003), showing that sardine spawn throughout the year but mainly have two spawning peaks, in early spring and autumn, and they have large temperature ranges from 14.5 to 21.5 °C in their spawning areas off the west of Cape Point. This is different for spawning peaks in Norwegian fish species, which might be influenced by the consistency of the "bottom-up" trophic effect in the Norwegian ecosystem. Southern Benguela fish species also showed a long duration of spawning while Norwegian fish species had short spawning durations. The consistent unexpected shifts in spawning times of Norwegian cod and Norwegian spring-spawning herring possibly indicate that environmental conditions influencing spawning strategies might be similar in the late 1990s and 2000s.

Cape hakes showed extended spawning periods in contrast to Arcto-Norwegian cod, which only spawn for three months. However, both of these demersal groups also showed unchanging spawning patterns over time, except shallow-water Cape hake, which extended its spawning period to autumn and winter from 2006 onwards (Figure 2.4e). In the Norwegian ecosystem, the inter-

annual consistency of the spawning period was associated with the seasonal light cycle being the main trigger for spawning (Sundby and Nakken, 2008). The timing and duration of spawning of cod have not been considered variable, although there are shifts in spawning peaks in some years (Sundby and Nakken, 2008; Olsen, 2010). Pedersen (1984) suggested that there was a delay in spawning in the 1980s and a long-term change in peak spawning. Delay in spawning times was not evident in the data from the 1980s, but it is evident in the late 1990s. This could indicate bias resulting from differences in methods used to analyze data. Similar to the Norwegian cod spawning times, other species of cod found in high latitude environments, such as northern Pacific cod (*Gadus macrocephalus*), are batch spawners with restricted spawning duration that begins in late February or early March (winter), and extends into early April (spring) (Neidetcher et al., 2014).

Spawning migrations of mature fishes are influenced by variability in oceanographic conditions. The possible environmental conditions influencing spawning migration in the southern Benguela are thermal stabilities, weak (upwelling-unfavourable) winds and nutrient limitations (Table 2.2). In contrast, Norwegian environmental factors that influence spawning migration include salinity stabilities, light limitations and south-westerly winds. This does not imply other physical conditions do not play a role. Southern Benguela fish species have a short migration route when moving to spawning grounds on the Agulhas Bank, whereas Norwegian fish species have a spawning migration period that is bi-seasonal because of the long migration route to spawning grounds off the Norwegian coastal banks. There was evidence (Table 2.2) that many migration routes are involved, resulting in long duration of migration. Another possible reason for long spawning migration of Norwegian spring-spawning herring is that it spawns in near-bottom waters (Rottingen, 1990; Huse et al., 2002; Skagseth et al., 2015), unlike southern Benguela anchovy and sardine which remain in the upper mixed layer (Boyd et al., 1992; Huggett et al., 2003). Although

the spawning migration of small pelagic fish species in these regions is short, deep-water Cape hake have long duration of migration to spawning grounds, similar to arcto-Norwegian cod (Table 2.2). The differences in environmental conditions influencing spawning migration off Norway and the southern Benguela (Table 2.2) are likely linked to the time of arrival of these species on the spawning grounds.

Conclusions

Most of the data collected from the literature show that spawning times and duration shift in both regions. However, the variability in the spawning times of species in each region is different, due to the physical dynamics influencing these ecosystems during spawning. The results are influenced by the fact that some years had no data, the methods used to assess spawning differ, including in the spatial and temporal coverage, and the techniques used differed. This probably introduced some bias, such as the "overestimation" of spawning duration in some species, patchness and scattering of the spawning times. There were also database limitations, such as inconsistency of selected surveys. For example, monthly and annual surveys were considered in combination and some of these surveys were conducted in different sites of both regions. Despite the weaknesses of the database, in a broad overview context there are patterns to be noted in both regions. Spawning times of southern Benguela fish species showed short-term and seasonal variability, probably linked to upwelling. Spawning patterns of Norwegian fish species were seasonally uniform with long-term variability, which depended on the primary production cycle and predator-prey interactions.

It is clear that there is more variability in spawning of southern Benguela fish species than Norwegian ones. However, there are also gaps in information about spawning peaks among years. The possibility of reviewing this case study again in future could be to synthesize scientific methods used in pelagic and demersal surveys in order to understand their influence on the current knowledge of reproduction success of these species. Improved understanding of the spatial coverage of reproduction habitats of these fish species will help in understanding the influence of spawning location on the timing of spawning.

CHAPTER 3: Biophysical characteristics of west coast nursery grounds of Cape hakes (*Merluccius paradoxus* and *Merluccius capensis*) in the southern Benguela upwelling ecosystem

Abstract

Environmental variables were investigated that could influence abundance and distribution of deep-water Cape hake (*Merluccius paradoxus*) juveniles on the Orange Banks nursery ground on the west coast of South Africa. Hydrographical observations (temperature, salinity, oxygen) accessed from annual Nansen demersal surveys were analysed in association with the abundance of deep-water Cape hake juveniles (length range 0–15 cm). Recruitment estimates of deep-water hake and shallow-water hake (*Merluccius capensis*) from a stock-recruitment model were correlated with alongshore wind speeds from combined satellite-derived (QuickSCAT and ASCAT) wind data from 1999–2015. Enhanced catches (>10000 fish.nmi^{-2}) occurred mostly between the Orange Banks and Hondeklip Bay during summer (January – March) surveys, particularly in 2003, 2005 and 2006. Catches were reduced (<5000 fish.nmi^{-2}) over the Orange Banks during summer in 2008 and 2009 surveys, However, in similar surveys (2008/2009) during summer, enhanced catches were noted off the Cape Peninsula (33-34˚ S). Near-bottom environmental variables (oxygen, temperature and salinity) varied in the surveys conducted during summer from inner to outer shelf waters. Near-bottom waters were cool with temperatures from 4 – 6˚C on the outer shelf and 8 – 9.5˚C on the mid to inner shelf. At the time of the surveys, the outer shelf waters were well-oxygenated (3.5 – 5 mL O_2.L^{-1}) with relatively low salinity (34 – 34.5), whereas in some areas, such as St Helena Bay (32-33˚ S), inner shelf near-bottom waters were hypoxic (< 2 mL O_2.L^{-1}) and showed relatively high salinity (34.7 – 35.1). Results of a single parameter quotient analysis indicated that deep-water Cape hake juveniles were disproportionately found in near-bottom waters that were oxygen-depleted to oxygenated (~2–4 mL O_2.L^{-1}) and were

disproportionately scarce when oxygen concentrations were very low (<2 mL O_2. L^{-1}) or high (>4 mL O_2. L^{-1}). There was a positive correlation between a deep-water Cape hake recruitment index and summer wind speed anomalies in the same year and autumn wind speed anomalies in the previous year. There was no similar correlation for shallow-water Cape hake. Strong northward winds occur during summer and spring on the Orange Banks and weaker winds during autumn and winter. The relationship between winds and near-bottom oxygen concentrations on the Orange Banks is unclear and needs to be investigated.

Introduction

Globally, hake species are targeted, commercially valuable fishes that support demersal fisheries and are important components of the ecosystem (Durholtz et al., 2015). The southern African region has three species of hake: *Merluccius paradoxus*, *Merluccius capensis* and *Merluccius polli* (Payne and Punt, 1985). The silver hake (*Merluccius polli*) is rarely found in the southern Benguela region as it only occupies the warmer waters of the Angolan substropical sub-system of the Benguela Current large marine ecosystem (Roel and Bailey, 1987; Wilhem, 2012; Durholtz et al., 2015). In addition, it is not as well-studied as the Cape hake species (*M. paradoxus* and *M. capensis*). The Cape hake species inhabit the northern and southern Benguela upwelling ecosystems (Crawford et al., 1980; Crawford, 1987). Geographically, the southern Benguela region extends south of 27°S to 36°S (near Cape Agulhas) and eastwards to Port Alfred (Kirkman et al. 2015). The seasonal variability of the oceanography in the southern Benguela west coast sub-system is evident in the four main upwelling cells, the Namaqua cell (30°S), the Cape Columbine cell (32.5°S), the Cape Peninsula cell (34°S) and the western Agulhas Bank cell (35°S) (Nelson and Hutchings, 1983). Cape hake juveniles mainly occupy nursery grounds on the west coast in the southern Benguela region (Strømme et al., 2015).

St Helena Bay has been identified as an important nursery area for juvenile hake found in the southern Benguela region (Hutchings et al., 2002; Grote et al., 2007). St. Helena Bay is located off the south-western coast of South Africa at a latitude of 32.5°S. This nursery area is known as a retention zone, where a seasonal oxygen minimum zone develops from summer through to autumn as a result of a combination of stratification, aerobic remineralisation and retention of organic matter (Pitcher and Nelson, 2006). In terms of spatial distribution, Stenevik et al. (2008) showed that the eggs and larvae of the two species of Cape hake drift in different ways, with deep-water

hake larvae mainly found further offshore. It has been concluded that the pelagic recruits of these two Cape hake species, therefore, occupy different nursery areas (Grote et al., 2007; Stenevik et al., 2008; Strømme et al., 2015).

As juvenile and adult hake often have different temperature tolerances and preferences (Olivar et al., 1988) in their habitats, the preferred ranges of other environmental variables (salinity and oxygen) may also vary. Oxygen concentrations in coastal upwelling water in the southern Benguela have been defined as "oxygen deficient" (< 1 mL $O_2.L^{-1}$), "hypoxic" (< 2 mL $O_2.L^{-1}$), "oxygen-depleted" (2 – 3 mL $O_2.L^{-1}$) and "oxygenated" (> 3 mL $O_2.L^{-1}$) (Monteiro et al., 2006). On the west coast of the southern Benguela, particularly in St Helena Bay, low levels of dissolved oxygen will induce stress in Cape hakes (Roel and Bailey, 1987; Hutchings et al., 2012). Unlike adult shallow-water Cape hake that can survive in low oxygen concentrations, deep-water hake adults are suggested to lack adaptation in oxygen deficient waters (Millar, 2000; Sundby et al., 2001). Temperature and oxygen are believed to have stronger influences than salinity on hake distribution and abundance (Olivar et al., 1988) although Botha (1986) suggested that hake catches depended on all three variables (bottom temperature, oxygen and salinity).

The reproduction processes involved in the life cycle closure of Cape hakes are complex and still require detailed understanding in terms of time and space. The locations of different life cycle stages of deep-water hake are depicted in Figure 3.1. The main spawning period of deep-water hake is between August and October, when the adult hake occupy the spawning grounds of the western Agulhas Bank (Durholtz et al. 2015). The physical factor that contributes to the transport of eggs and larvae after spawning is the Benguela coastal jet. This transport mechanism is enhanced by equatorward winds during summer for a minimum period of 45 days, when larval transport of Cape hake occurs and the alongshore south-easterly winds are important for transport

success (Grote et al., 2007; Garavelli et al., 2011; Grote et al., 2012). The wind strength influences the vertical movement of larvae as they passively disperse to surface layers (Shannon et al., 1988). Beyond this period, offshore losses are experienced as deep-water hake larvae begin to be recruited to the pelagic zone (Stenevik et al., 2008).

Deep-water hake juveniles reach nursery grounds during January/February (Grote et al., 2010) on the west coast (Figure 3.1). Coastal upwelling conditions in the Cape Columbine upwelling cell play an important role in enhancing primary productivity; local currents also favour good retention for deep-water hake juveniles in St. Helena Bay. Some juveniles migrate northwards, where they end up settling on the Orange Banks (29°S – 31°S) (Strømme et al., 2015). St Helena Bay is well-known as an important nursery area for a variety of fish species (Hutchings et al., 2002; Stenevik et al., 2008), but the Orange Banks area has not been intensively studied. The aim of this study was to investigate the environmental variables that could influence the suitability of the Orange Banks as a nursery area for deep-water hake juveniles (*Merluccius paradoxus*).

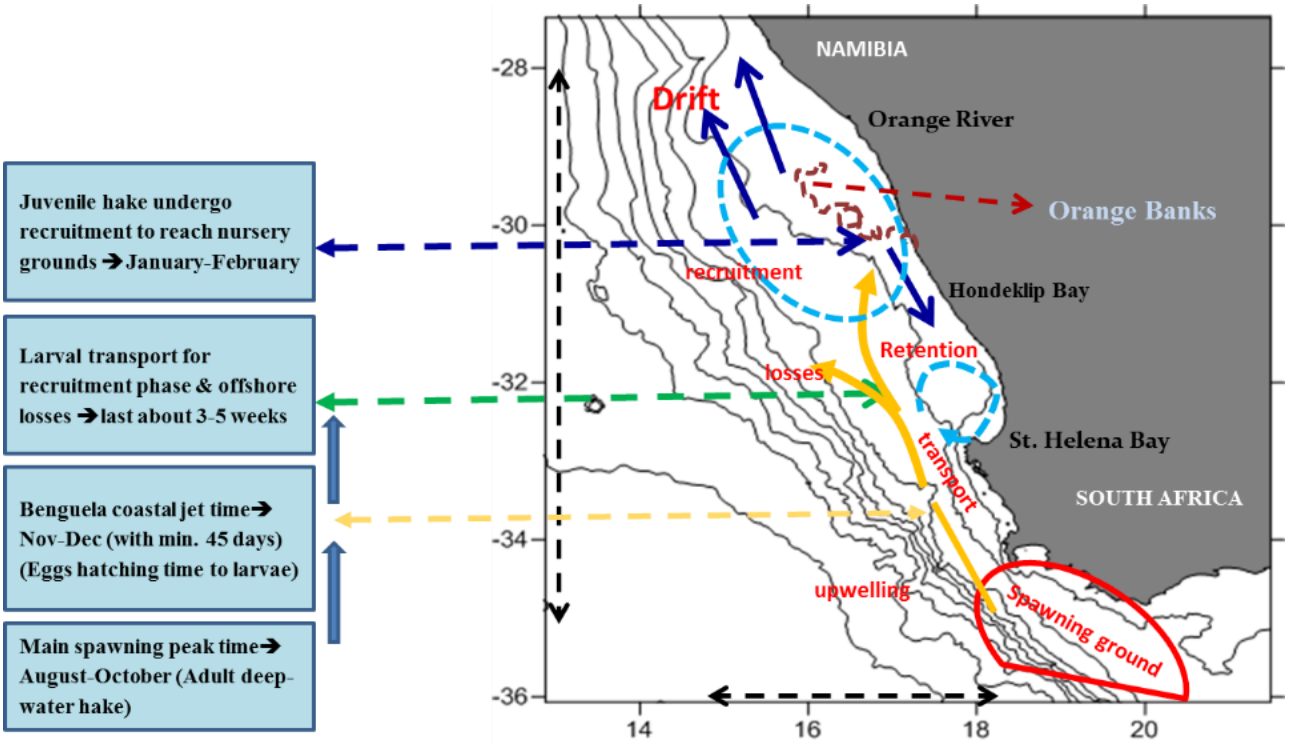

Figure 3.1: Schematic map of the west coast sub-system of the southern Benguela, showing the location of key events involved in the life cycle of deep-water Cape hake (*Merluccius paradoxus).* (Modified from findings of Grote et al., 2007; Stenevik et al., 2008; Grote et al., 2012; Garavelli et al., 2012; Strømme et al., 2015).

Methods

Survey design and data sources

Annual demersal surveys were obtained from the Ecosystem Approach to Fisheries (EAF) Nansen programme. These surveys conducted in the Benguela upwelling system were all geo-referenced (spatial location in latitude and longitude) and they were multivariate (included fish data and physical data collected at each sampled transect station). Strømme et al. (2015) and Johnsen and Axelsen (2015) explained full details of gear used, survey design and structuring of surveys, and the quality of data used in this study is discussed below. The depth locations of the shelf areas for this study are based on Sundby et al. (2001) and Hutchings et al. (2002) as follows: inner shelf (25 – 200 m), mid-shelf (200 – 400 m) and outer shelf (400 - 1000 m). Data were accessed through the NANSIS database at the National Marine Information and Research Centre (NatMIRC) of the Ministry of Fisheries and Marine Resources, Namibia. The Fisheries Branch of the Department of Agriculture, Forestry and Fisheries provided the recruitment data of Cape hake species (Rademeyer and Butterworth, 2013).

Demersal surveys were mostly conducted in summer (January-February), but a few were carried out in May and October. The research vessel used in South African waters from the Orange River to Cape Agulhas was the RV Fridtjof Nansen (Strømme et al., 2015). From 2003-2013 the timing of these surveys and their geographical coverage were adjusted; this causes some inconsistency in the spatial distributions described below as only 2010 had full coverage. Demersal trawling surveys conducted in South Africa followed a random stratified sampling survey design. The hake sampling in South Africa conducted on board the R/V Dr Fridtjof Nansen mainly focused on the distribution of deep-water hake (*Merluccius paradoxus*), although the surveys also monitored shallow-water hake (*Merluccius capensis*). The catch rates for different length classes from the

demersal trawling surveys are the same as those used by Strømme et al. (2015). The hydrographical data on temperature, salinity and oxygen were collected with a CTD (conductivity-temperature-depth) *Seabird 9 plus* probe between the surface and 10 m off the bottom. CTD casts were made prior to each trawl station.

Estimated numbers of recruited Cape hake juveniles per year were obtained from the results of a stock-recruitment estimation model from 1980 – 2015 (Rademeyer and Butterworth, 2013). Recruitment estimates were standardized here, such that the mean number of recruits from the model time series was subtracted from each estimated value and divided by the standard deviation, forming a recruitment index.

Two scatterometer data sets obtained from an internet source (http:// www.remss.com/ missions/ QuikScat wind vectors) provided sea wind products. These datasets were the NASA quick scatterometer (QuikSCAT), which was initiated in 1999 and continued through 2009, and the advanced scatterometer (ASCAT), which was available from 2007–2016. QuikSCAT data have a high resolution: 0.25˚ x 0.25˚. The QuikSCAT and ASCAT wind products overlapped between 2007 and 2009; they were averaged for this period, providing a merged data product in a single dataset. Wind data were extracted along a line with meridional (north – south) and zonal (east – west) directional components, extending between longitude 14.80°E to 18.30°E and latitude 28.0°S to 35.0°S.

Data processing

The numbers of hake juveniles per square nautical mile (nmi^{-2}) were estimated by converting catch per trawl (number of fish caught) to fish densities ($fish.nmi^{-2}$). For each station, a sample of fish was taken and each fish measured to the nearest 1 cm total length (TL) and weighed to the nearest gram. All samples of small hake were checked for species identity using counts of vertebrae (usually 50 fish were examined). This method was independently verified by genetic screening (Matthee and Gopal, 2004; unpublished report of the University of Stellenbosch, South Africa; Matthee, pers. comm.). The ratio of fish numbers in a length range (0 – 15 cm) relative to the total numbers, RATIO (L_{min}, L_{max}), was multiplied by the total catch of a given species to give Catch (L_{min}, L_{max}), yielding the total number of that length group in the catch, where L_{min} is the minimum fish length (1 cm) and L_{max} is the maximum fish length (15 cm) in the length range. RATIO is a non-dimensional coefficient whereas catch signifies the total number of fish caught.

$$\text{Catch } (L_{min}, L_{max})(\text{no. of fish}) = \text{RATIO } (L_{min}, L_{max}) * \text{Catch (no. of fish)} \quad \text{.....(1)}$$

The effective fishing area (swept area, nmi^2) was calculated as the product of the linear mouth opening of the net (18.5 m, set for the Nansen surveys) and the haul length, based on GPS readings, all converted to nautical mile units:

$$\text{Swept Area } (nmi^2) = \text{Trawl distance (nmi)} * \text{wing span (nmi)} \quad \text{.....(2)}$$

The catchability coefficient (q), i.e. the fraction of the fish encountered by the trawl that was actually caught, was assumed equal to 1. To estimate the fish density in each length range at each trawl station, Catch (L_{min}, L_{max}) was divided by the swept area:

$$\text{Fish density } (L_{min}, L_{max}) \ (fish.nmi^{-2}) = \frac{\text{Catch (Lmin,Lmax)(number of fish)}}{\text{Swept Area } (nmi^2)} \quad \text{.....(3)}$$

Statistical analysis

Spatial displays and contour maps from biological and physical data were generated based on kriging principles. Using the geostatistical software package SURFER 13® for Windows (Golden Software Inc.), a kriging interpolation plan was set up in which spatial interpolation was used to predict values of near-bottom environmental variables and their locations.

Single Parameter Quotient (SPQ) analysis, as described by Drapeau (2004), was applied using R statistical scripts (R core team 2015) to examine habitat characteristics of deep-water Cape hake juveniles (in terms of near-bottom oxygen concentrations) for three different juvenile length classes: small (< 15 cm), medium (16-35 cm) and large (36-50 cm). The range of near-bottom oxygen values was divided into n=12 categories and the relative frequencies of observations of oxygen (O_c) in each category (c) were determined as follows:

$$\%O_c = \frac{O_c}{\sum_{c=1}^{n} O_c} * 100 \quad \text{..... (4)}$$

Fish density data were similarly analysed, where the number of fish caught per square nautical mile (fish.nmi^{-2}) were associated with each near-bottom oxygen category (O_c) and expressed as a percentage of the total fish density (F_c) of deep-water Cape hake juveniles.

$$\%F_c = \frac{F_c}{\sum_{c=1}^{n} F_c} * 100 \quad \text{.....(5)}$$

The percentage of total fish density in each near-bottom oxygen category was divided by the percentage of occurrence of near-bottom oxygen categories to calculate the single parameter quotient value, Q_c:

$$Q_c = \frac{\%F_c}{\%O_c} \quad \text{..... (6)}$$

The Q_c value essentially represents over- or under- representation of fish density within the near-bottom oxygen categories, giving a value of one if distribution is random. Bootstrapping methods were used to compute the upper and lower 95% confidence intervals of the quotient values. Quotient values greater than the upper confidence interval are considered to signify positive association (deep-water hake juveniles occur more often than would be expected by chance in those oxygen ranges), whereas Q_c values less than the lower confidence interval indicate negative association (deep-water hake occur less often than would be expected by chance in those oxygen ranges). Summaries of quotient curves for near-bottom oxygen concentrations are in the Appendices (Figure A1).

Wind velocity data from the two satellite-based data sets provided weekly-scale wind data from 1999–2016, which were rotated and converted to alongshore components. A wind index was calculated that represented the average wind conditions over the outer shelf between Cape Columbine and the northern end of the Orange Banks. Wind velocity anomalies were calculated by finding the difference between alongshore wind speed of each year and the average wind speed from 1999–2015. The weekly wind speed data anomalies were further averaged to produce seasonal wind speed anomalies for each year from 1999 -2015 for comparison with the annual recruitment estimates. Values of recruitment indices of both Cape hake species from 1999 – 2015 and seasonal wind speed anomalies were standardized. Pearson correlation coefficients were calculated using Excel (Microsoft ® package 2010) to evaluate the relationship between the seasonal wind speed anomalies and recruitment indices for both Cape hake species using two lags. The first lag represents the relationship between recruitment and wind before spawning (Lag = 0 year) and the second lag represents the relationship between recruitment and wind after spawning (Lag = 1 year). Scatterplots of the data for correlation analysis are in the Appendices (Figure A2).

Data quality

Full geographic coverage of deep-water Cape hake did not occur in all the survey years. Only in one year (2010) was there complete coverage (Strømme et al., 2015). The survey data were mostly confined to the west coast of the southern Benguela, with few data from the south coast. Some data were also missing, because the CTD data were truncated near the seabed at a fixed height of 0m above the lowest CTD depth (25 m). It also was not possible to include contour maps for the distribution of shallow-water Cape hake because spatial coverage was limited and this species was absent in many surveys; the bottom trawl surveys focused on deep-water Cape hake.

Results

Spatial and temporal distribution of deep-water hake juveniles and physical factors

There is spatial and temporal variation in deep-water Cape hake distribution throughout the years of the Nansen surveys (Figure 3.2). Demersal trawling surveys conducted from 2003 – 2013 show enhanced catches of deep-water Cape hake being confined in patches along the west coast nursery ground, particularly between Hondeklip Bay and the Orange Banks. This excludes the distribution of hake juveniles in Figure 3.2 (h) and (o) for surveys conducted in 2007 and 2009, where hake juveniles are mostly absent. In most years of the Nansen surveys conducted in summer there are greater catches (> 10 000 fish.nmi^{-2}) of hake juveniles off the Orange Banks (29ºS – 31ºS) than in the other nursery areas. During summer surveys conducted in 2007 – 2010 the hake juvenile catches are reduced (< 5000 fish.nmi^{-2}). The two Nansen surveys conducted in 2004 and 2005 during spring show distinct spatial distributions of deep-water Cape hake; in 2004 they are concentrated (~15 000 fish.nmi^{-2}) on the northern part of the Orange Banks (29ºS – 31ºS) but in 2005 they are concentrated (>15 000 fish.nmi^{-2}) in the Namaqua region. There was limited geographical coverage in the south for the 2004 survey and the 2005 survey occurred north of South Africa.

There is spatial and temporal variability in the near-bottom temperature distributions in most of the years (Figure 3.3). There are temperature discrepancies from the inner to outer shelf waters along the west coast in all the survey years. In the Nansen surveys conducted during summer, mid- to inner shelf waters were warm, with temperatures ranging from 10 – 16ºC. Outer shelf waters were cold, with temperatures ranging from 4 to 5. ºC, similar to the surveys conducted in spring (2004 – 2005) and autumn (2007). During summer surveys in 2009 and 2010 mid-shelf waters were cool, with a temperature range of 6 – 9 ºC. Near-bottom salinity distributions did not vary

much throughout the years of the Nansen surveys (Figure 3.4). In most years of the surveys conducted in summer, mid- to inner shelf waters were more saline (> 34.5) than outer shelf waters (< 34.4). This is similar to the surveys conducted during spring and autumn in 2004 – 2005 (Figure 3.4 (m) and (n)) and 2007 (Figure 3.4o). This is different for the survey conducted during summer in 2009, when mid-shelf water was less saline, with a salinity range of 34.4 – 34.5.

There is more intense spatial and temporal variability in the near-bottom oxygen distributions (Figure 3.5). In most surveys, inner shelf water was hypoxic (< 2 mL $O_2.L^{-1}$) along the west coast, mid-shelf water was oxygen-depleted (2 – 3 mL $O_2.L^{-1}$) and outer shelf water was well oxygenated (> 3 mL $O_2.L^{-1}$). This is different for the 2009 survey conducted in summer (Figure 3.5h), where mid-shelf water showed a patch of hypoxic conditions over the northern part of the Orange Banks (30ºS).

In the three sub-regions along the west coast: Orange Banks (29ºS – 31ºS), Namaqua (31ºS – 33ºS) and Cape Peninsula (33ºS – 34ºS), hake juveniles are mostly distributed in the mid-shelf waters (Figure 3.2) in most years. Enhanced catches of hake juveniles in most years over the Orange Banks are associated with warm, saline, mid-shelf water that is oxygen-depleted, while off the Cape Peninsula they are associated with well-oxygenated conditions (Table 3.1). In most years, reduced catches of hake juveniles are mostly observed off the Namaqua region compared to the Orange Banks and Cape Peninsula, and are associated with warm, saline, well-oxygenated mid-shelf water. However, this is different over the Orange Banks, where they are associated with hypoxic mid-shelf water in 2009. In 2008 – 2009, small catches of hake are associated with warm, saline, mid-shelf water, with varied oxygen concentrations over the Orange Banks and Namaqua region, while off the Cape Peninsula there were greater catches linked to warm, saline, well-oxygenated mid-shelf water.

Table 3.1: Spatial and temporal analysis of near-bottom environmental factors (temperature=T, salinity=S and oxygen=O_2) in association with small deep-water Cape hake (< 15 cm) catches from 2003 – 2013 surveys of R/V Dr Fritjof Nansen during summer in three different regions: Orange Banks (highlighted in orange), Namaqua (grey) and Cape Peninsula (blue). Hake abundance categories: High = H (> 15 000 fish.nmi^{-2}), medium = M (< 15 000 fish.nmi^{-2}),) and low = L (< 5000 fish.nmi^{-2}). Warm temperatures = W (10 – 16 ºC), cold temperatures = C (3 – 9 ºC). High salinity water = H (34.5 – 35) and low salinity water = L (< 34.5). Oxygen concentration categories are represented as 1= hypoxic, 2=oxygen-depleted and 3=well oxygenated.

Regions	**Orange Banks (29ºS – 31ºS)**						**Namaqua (incl. Cape Columbine cell) (31ºS – 33ºS)**						**Cape Peninsula (33ºS – 34ºS)**					
Years	**Small hake abundance (H/M/L)**	**T**	**S**	**O_2**			**Small hake abundance (H/M/L)**	**T**	**S**	**O_2**			**Small hake abundance (H/M/L)**	**T**	**S**	**O_2**		
				Inner shelf	mid-shelf	outer shelf				Inner shelf	mid-shelf	outer shelf				Inner shelf	mid-shelf	outer shelf
2003	H	W	H	1	3	3	L	W	H	1	3	3	H	W	H	2	3	3
2004	H	W	H	2	2	3	–	–	–	–	–	–	–	–	–	–	–	3
2005	H	W	H	1	2	3	H	W	H	1	3	3	H	W	H	2	3	3
2006	H	W	H	1	2	3	H	W	H	1	2	3	H	W	H	2	3	3
2007	H	W	H	1	2	3	M	W	H	–	3	3	M	W	H	2	3	3
2008	L	W	H	1	2	3	L	W	H	1	3	3	H	W	H	2	3	3
2009	L	C	L	2	1	3	L	W	H	1	2	3	H	W	H	2	3	3
2010	M	C	H	2	2	3	H	C	H	1	2	3	M	C	H	3	3	3
2011	M	W	H	2	2	3	H	W	H	1	3	3	L	W	H	2	3	3
2012	M	W	H	2	2	3	H	W	H	2	3	3	H	W	H	3	3	3
2013	H	W	H	1	2	3	L	W	H	1	2	3	L	W	H	3	3	3

– No data

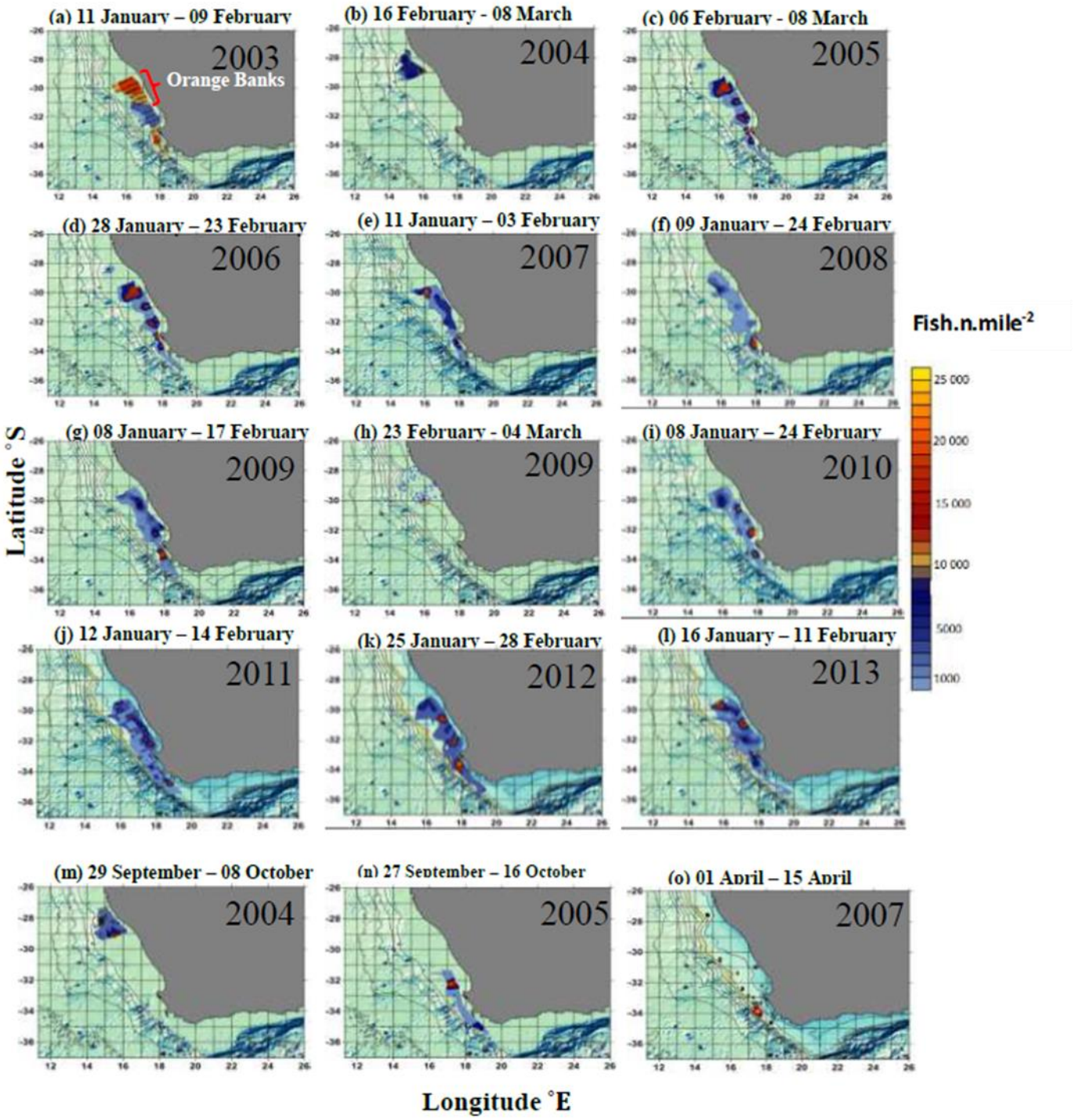

Figure 3.2: Distribution of deep-water Cape hake juveniles (< 16 cm) from Nansen surveys during (a) – (l) summer (January – March), (m) and (n) spring (September – October) and (o) autumn (April) from 2003 – 2013.

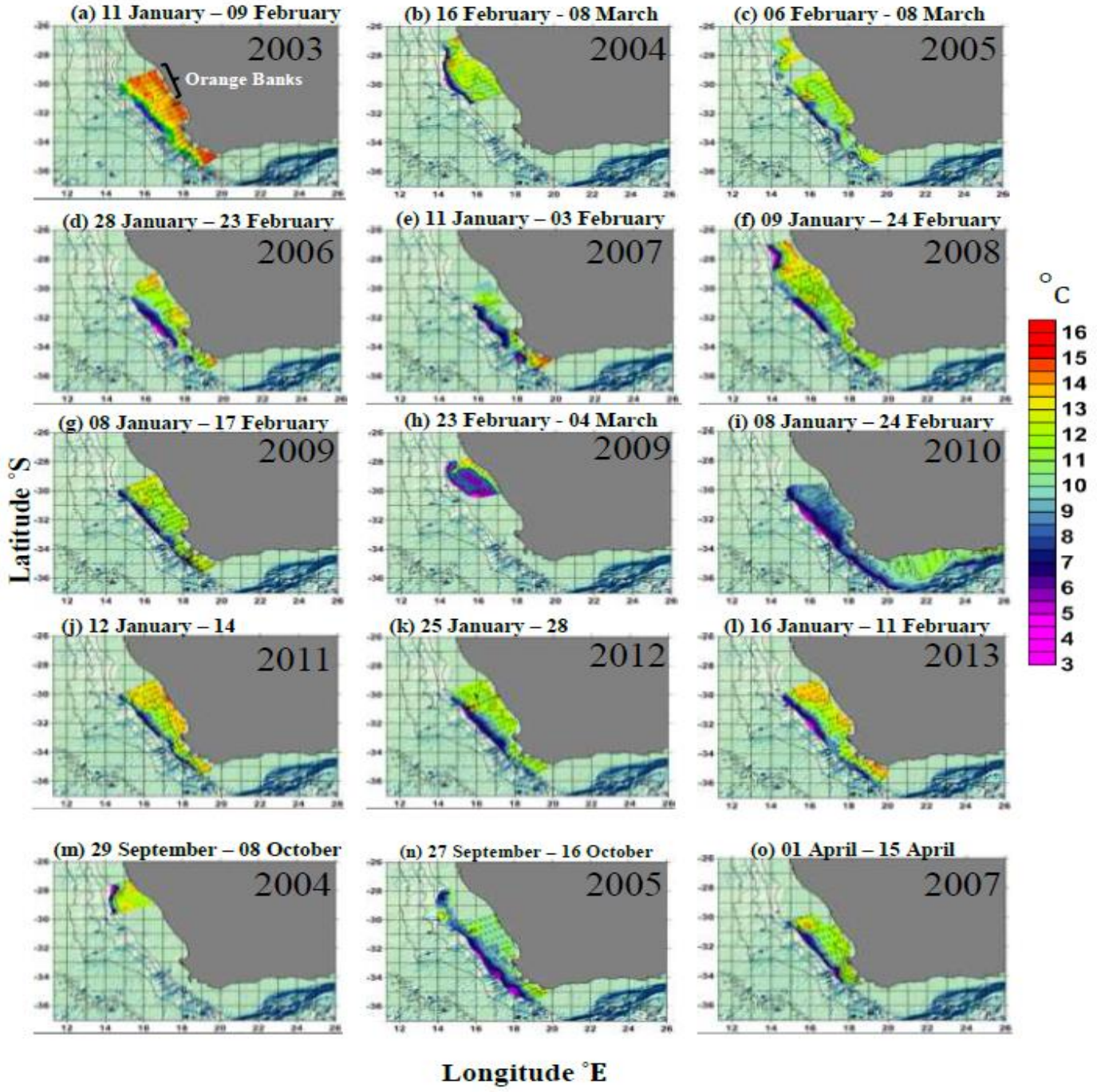

Figure 3.3: Distribution of near-bottom temperature (˚C) from Nansen surveys during (a) – (l) summer (January – March), (m) and (n) spring (September – October) and (o) autumn (April) from 2003 – 2013.

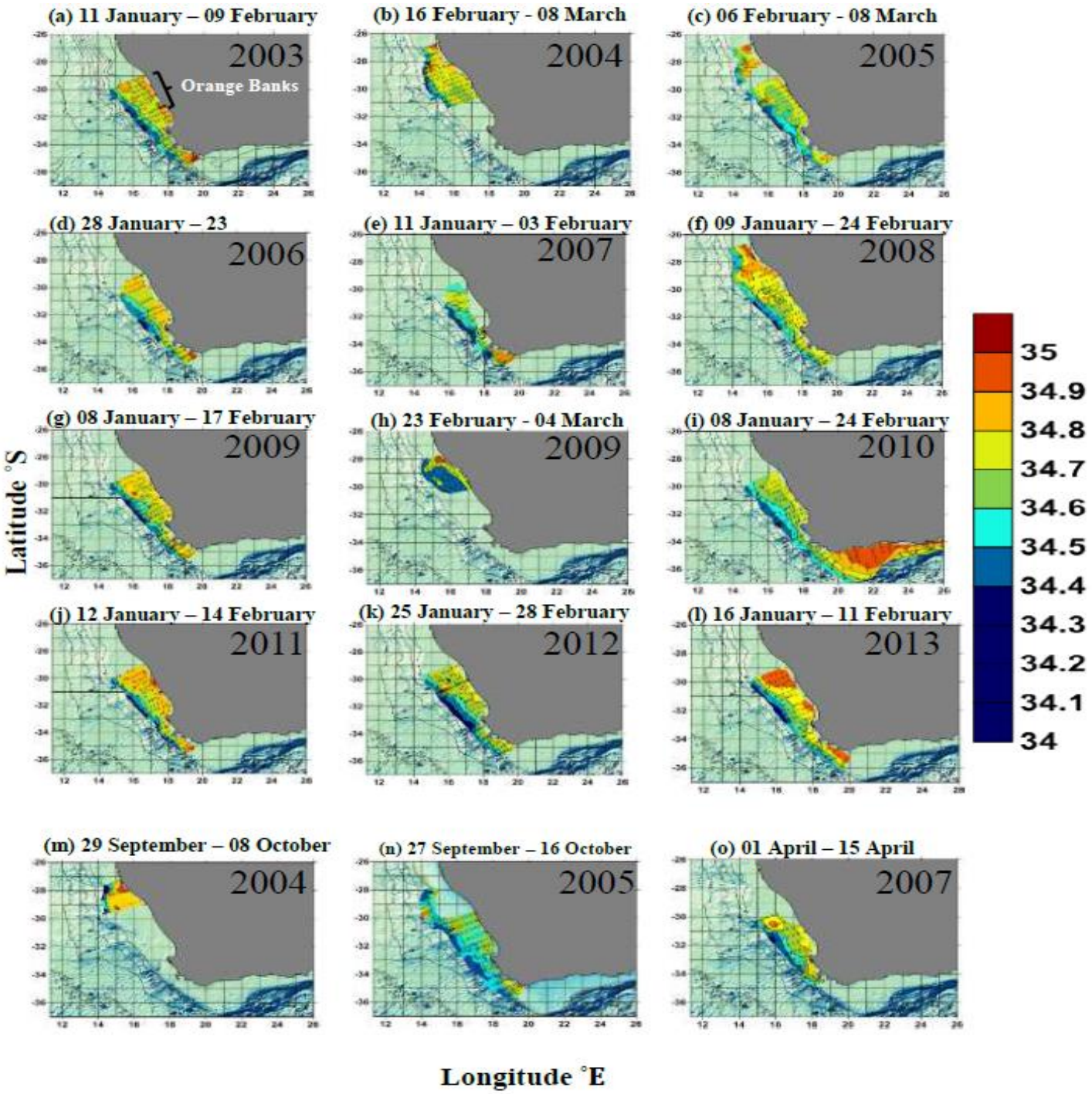

Figure 3.4: Distribution of near-bottom salinity (ppt) from Nansen surveys during (a) – (l) summer (January – March), (m) and (n) spring (September – October) and (o) autumn (April) from 2003 – 2013.

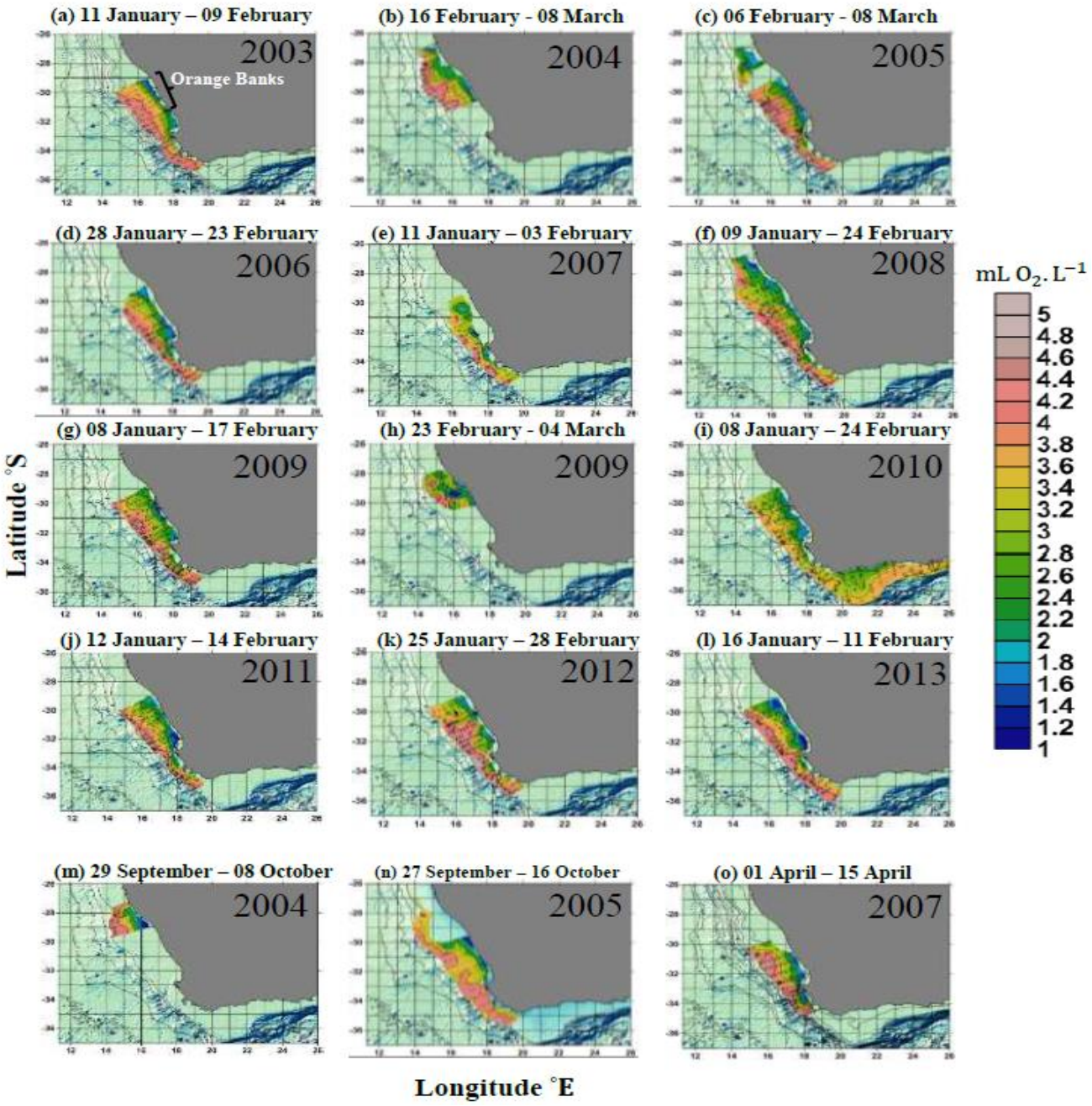

Figure 3.5: Distribution of near-bottom oxygen (ml $O_2.L^{-1}$) from Nansen surveys during (a) – (l) summer (January – March), (m) and (n) spring (September – October) and (o) autumn (April) from 2003 – 2013.

Association of deep-water Cape hake with near-bottom oxygen concentrations differed depending on length class (Figure 3.6). Small deep-water Cape hake juveniles (< 15 cm) occur in association with hypoxic, oxygen-depleted to oxygenated (1.25 – 3.75 mL $O_2.L^{-1}$) waters (Figure 3.6a) but are disproportionately found in well-oxygenated bottom waters. Medium-sized fish (16 – 35 cm) also mainly occur in near-bottom waters that are oxygenated and oxygen-depleted, and are disproportionately found in water with high oxygen concentrations (Figure 3.6b) compared to small-sized fish. This is completely different for the large fish (36 – 50 cm), which are hardly found in oxygen-depleted near-bottom water, occur disproportionately in high oxygen near-bottom water (Figure 3.6c).

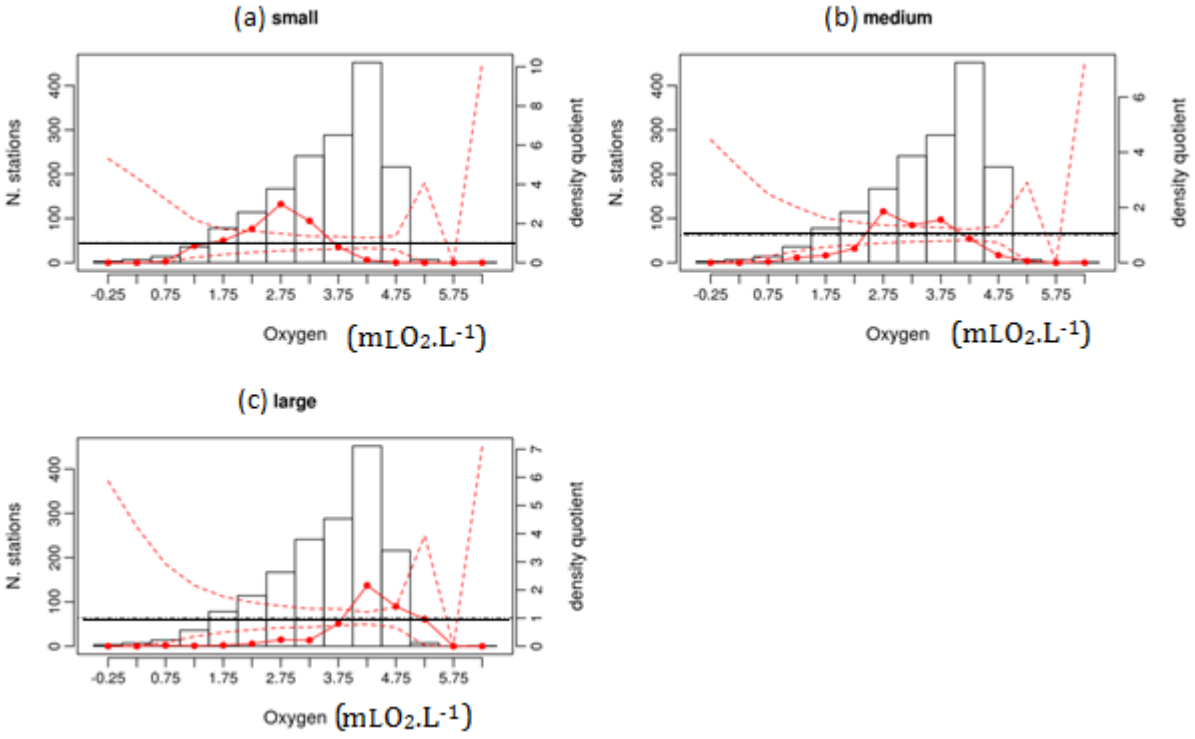

Figure 3.6: Frequency distribution (histograms) of near-bottom oxygen for Nansen surveys (2003 – 2013) combined. Quotient curves (lines with black markers) are shown for deep-water hake for different length class ranges: (a) small (0 – 15 cm), (b) medium (16 – 35 cm) and (c) large (36 – 50 cm). A quotient value of 1 is plotted along with 95 % confidence intervals (red dotted line).

Variability in recruitment indices and upwelling-favorable wind speed anomalies

The recruitment index of deep-water Cape hake varied over the years (Figure 3.7). The index was generally positive in the 1980s, the early 1990s and in the mid-2000s, and negative in the late 1990s, early 2000s and in recent years. Largest values occurred in 1994 and 2004 and smallest values in 1985 and 2009.

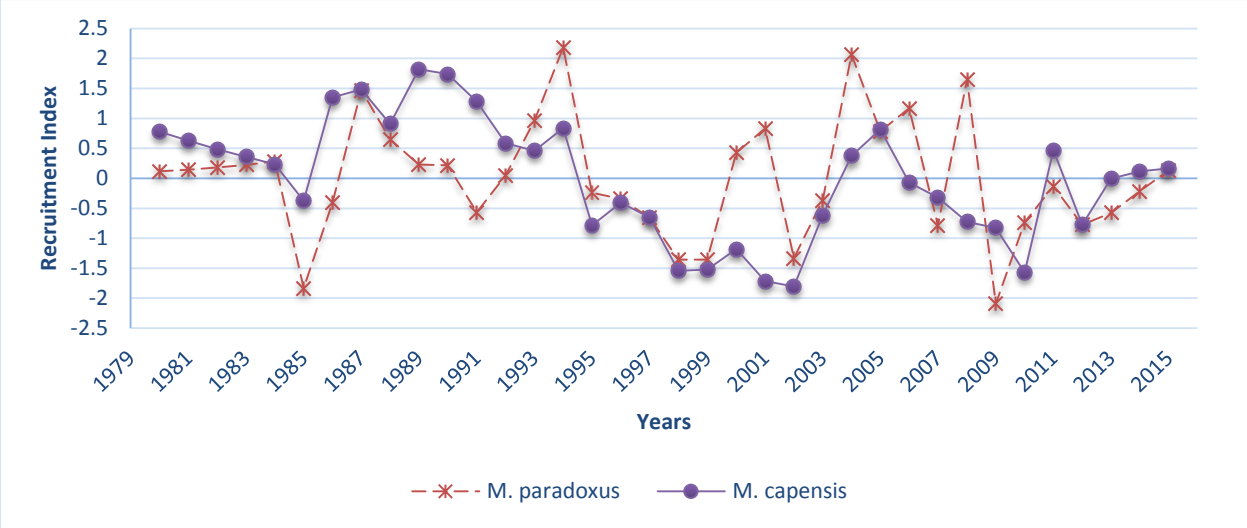

Figure 3.7: Time series of recruitment indices for *Merluccius capensis* and *Merluccius paradoxus* from 1980 – 2015.

Figure 3.8 shows a Hovmöller diagram depicting the seasonal cycle of the meridional wind between the Cape Peninsula and the northern extent of the Orange Banks during 1999-2016. Winds along the west coast were strong during spring and summer (October – March), when the wind velocities were 6 – 7 $m.s^{-1}$. Winds are strong, blowing northwards during these seasons off the Cape Peninsula (33˚S – 35˚S), Namaqua region (33˚S – 31˚S), Orange Banks (29˚S – 31˚S) and south of Lüderitz (28˚S – 29˚S). Strong southward winds are observed during autumn and winter (April – August) off the Cape Peninsula to Namaqua, but are somewhat weaker off the Orange Banks.

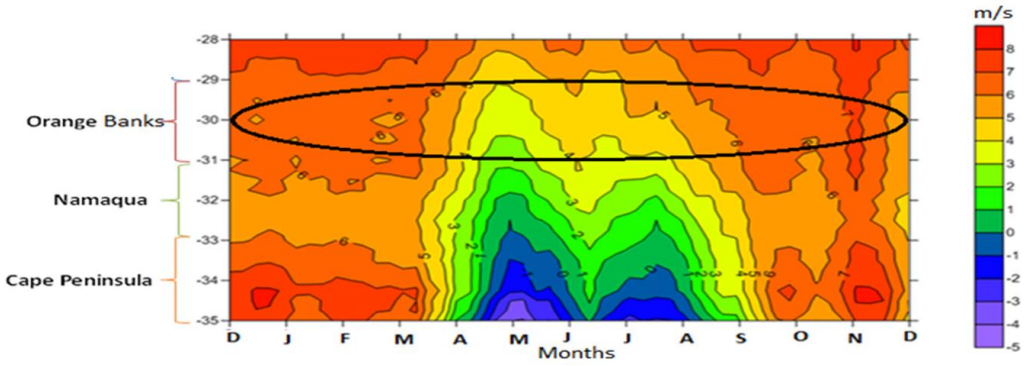

Figure 3.8: Seasonality of wind speeds along the west coast region. The colour bar illustrates wind velocity (in $m.s^{-1}$).West coast latitudes are sub-divided into three areas.

The evolution of meridional wind anomalies from 1999-2016, averaged for the west coast of South Africa, is shown in Figure 3.9. The time-series is dominated by intra-seasonal anomalies, typically in the range ±2 m s^{-1}, and does not show a long term trend. On inter-annual time-scales, the longest period of southward negative meridional wind anomalies was observed between 2008 and 2010, whereas the strongest northward positive wind anomaly took place in 2003. Reduced positive wind speed anomalies are observed from 2013 – 2015, whereas reduced negative wind speed anomalies are noted from 2004 – 2006.

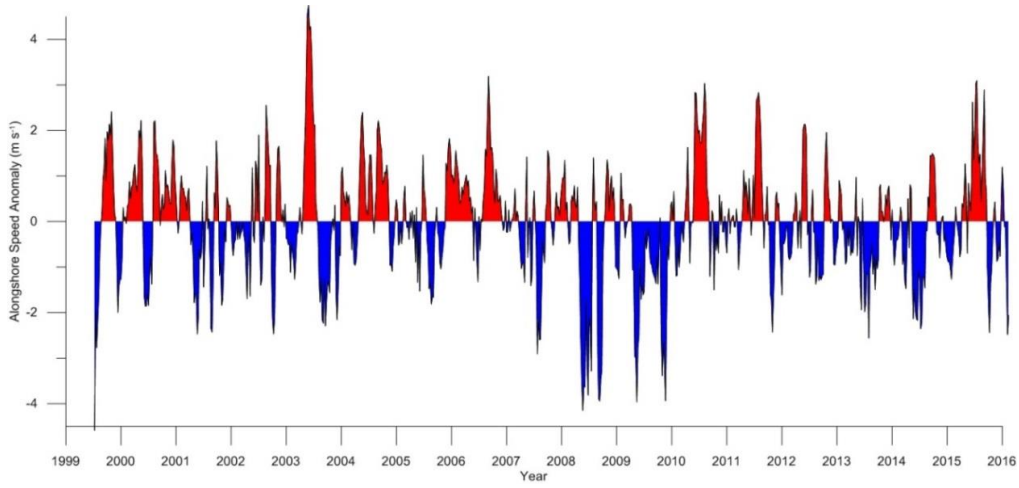

Figure 3.9: Time series of wind speed anomalies along the west coast of the southern Benguela (1999 – 2015).

Relationship between recruitment and the wind speed anomalies

There was a positive correlation between the recruitment index for deep-water Cape hake and summer wind speed anomalies in the same year and autumn wind speed anomalies in the previous year (Table 3.2). There were no significant correlations for shallow-water Cape hake (Table 3.2).

Table 3.2: Results of correlation analyses between seasonal wind speed anomalies and recruitment indices of two Cape hake species divided. The two lags correlate recruitment with wind speed anomalies in the same year (Lag = 0 year) and the previous year (Lag = 1 year).

Merluccius paradoxus				
Lag=0 year				
Seasons	**r**	**df**	***p***	**Significance**
Summer	0.48	16	0.0492	Significant
Autumn	0.18	16	0.5175	Non-significant
Winter	0.05	16	0.8466	Non-significant
Spring	0.26	16	0.3119	Non-significant
Lag= 1 year				
Summer	0.40	15	0.1296	Non-significant
Autumn	0.56	15	0.0253	Significant
Winter	0.32	15	0.2219	Non-significant
Spring	0.08	15	0.7477	Non-significant
Merluccius capensis				
Lag= 0 year				
Seasons	**r**	***df***	***p***	**Significance**
Summer	0.32	16	0.2178	Non-significant
Autumn	0.02	16	0.9394	Non-significant
Winter	0.13	16	0.6138	Non-significant
Spring	0.02	16	0.9501	Non-significant
Lag= 1 year				
Summer	0.05	15	0.8408	Non-significant
Autumn	0.22	15	0.4197	Non-significant
Winter	0.18	15	0.5166	Non-significant
Spring	0.28	15	0.2915	Non-significant

Discussion

Influence of near-bottom environmental factors on the spatial distribution of hake juveniles

From the survey data presented, it is evident that there is spatial and temporal variability in the catch rates of deep-water Cape hake, probably influenced by near-bottom environmental factors (Wieland et al., 2012). Greater catches of deep-water Cape hake juveniles were mostly confined to the mid-shelf waters off the Orange Banks and Cape Peninsula. This indicates that the Orange Banks is a suitable habitat for juveniles of this species. This finding was also captured in Strømme et al. (2015), where small juveniles (<16 cm) were noted to occur consistently in high abundance between Hondeklip Bay and the Orange Banks, suggesting that this is an important nursery area for this species.

In 2008 – 2010 and 2012, the demersal surveys conducted during summer (January – March) did not indicate the Orange Banks as a nursery habitat for deep-water Cape hake juveniles, because reduced catches were observed. In contrast, in the Namaqua region, there was a confined enclave with high abundance of hake juveniles in those years. This may suggest that there was poor recruitment of deep-water Cape hake juveniles on the Orange Banks as compared to the Namaqua region, or there might be environmental conditions that influenced the spatial distribution of these juveniles, which are still not well understood and require further investigation. Nursery grounds of deep-water Cape hake juveniles were located up to Hondeklip Bay in Pillar and Barange's, (1995) study. The timing of appearance of deep-water Cape hake juveniles in the nursery areas was limited during the survey conducted in April. This does not imply that there were no hake at all; however, it means that during the deployment of bottom trawls, hake juveniles were absent and mostly adult hake were caught. Most spatial distributions of near-bottom temperature and

salinity from mid-shelf waters off the Orange Banks did not vary much throughout the surveys, mainly showing warm, saline waters. This stability in the inter-annual variability of physical factors is supported by Bakun (2010), Ostrowski et al. (2011), Wieland et al. (2012) and Hutchings et al. (2012), suggesting that stable near-bottom environmental conditions are likely to play a role in creating favourable environments for the deep-water hake juveniles in their early stages. This is similar to the preferential distribution of European hake (*Merluccius merluccius*), although deep-water Cape hake juveniles occupy a different environment to the north Atlantic ecosystem. Sánchez and Gil (2000) reported that juveniles of *Merluccius Merluccius* occupy nursery areas with stable hydrographic conditions until spring and their inter-annual variation in abundance is always strong

Biophysical characteristics influencing nursery areas of Cape hakes

Physical variability was observed in near-bottom oxygen concentrations in association with spatial distributions of deep-water Cape hake juveniles. The near-bottom waters in the mid- to inner shelf were hypoxic or showed oxygen depletion off the Orange Banks nursery ground. These waters contained hake juveniles in greater than expected relative abundance. The consumption of oxygen during the decay of phytoplankton could explain oxygen depletion on the nursery ground found off the southern Benguela during summer/autumn (Monteiro et al., 2006). Results from the single parameter quotient analysis show that oxygen variability in near-bottom waters of west coast nursery areas in the southern Benguela could possibly influence small deep-water Cape hake juveniles (< 16 cm). Small deep-water Cape hake juveniles were observed to occur in near-bottom waters with hypoxic conditions (< 2 mL $O_2.L^{-1}$) but were disproportionately associated with oxygen depleted water (2 – 3 mL $O_2.L^{-1}$). They were disproportionately absent from water with higher oxygen concentrations (> 3 mL $O_2.L^{-1}$). This supports the findings of Wieland et al. (2012)

that adult shallow-water Cape hake use oxygen-depleted bottom water as a refuge, so they have better conditions for survival, and they tend to overlap with juvenile deep-water Cape hake in terms of depth and spatial distribution. The opposite occurs for medium-sized hake juveniles that have grown in length, which appeared to be disproportionately scarce in hypoxic near-bottom waters. Similar to the deep-water Cape hake juveniles, higher densities of southern hake *(Merluccius hubbsi*) juveniles found off the Malvinas/Falkland Islands occupy waters with low oxygen concentrations (< 3 mL $O_2.L^{-1}$) (Bustos et al., 2007). Millar (2000) explained that large hake are not able to take up oxygen as efficiently as smaller fish, since fish gills do not grow as fast as the body (Pauly, 1998). Therefore, oxygen limitation is not good for large hake juveniles. The disproportionate occurrence of small deep-water Cape hake in oxygen-depleted water supports Roel and Bailey (1987), who speculated that deep-water Cape hake juveniles cannot tolerate oxygen deficiency. Jarre et al. (2015) noted a restricted spatial coverage of lower oxygen concentrations off Hondeklip Bay that appear to merge with oxygen-depleted water over Orange River mouth. The extension of oxygen-depleted water from these areas (Hondeklip Bay and Orange River mouth) towards the Cape of Good Hope could occur if the coastal countercurrent were to carry low concentrations that far. Conclusions about spatial coverage limits could not be drawn in Jarre et al. (2015), as further investigation is required. Based on Jarre et al. (2015), it can be assumed for this study that depending on the size of deep-water hake juvenile and the level of depth in which they are settling on the water column, the oxygen-depleted water off Orange River mouth probably has less influence on their recruitment from causing them to recruit away from the coast.

Variability in recruitment and wind speed anomalies

The inter-annual variability in the time series of recruitment indices for Cape hake species shows some trend. In contrast, intra-seasonal rather than inter-annual variability dominates the pattern observed in upwelling favourable winds. The impact of intra-seasonal fluctuations in upwelling-favourable winds on *M. paradoxus* recruitment is shown by the correlation analyses (Table 1). Recruitment success of deep-water Cape hake tends to be associated with positive wind anomalies during the summer and during the preceding autumn. Given the importance of oxygen concentrations for the species, it is possible there is a relationship between winds and near-bottom oxygen concentrations on the Orange Banks. This aspect needs further investigation.

Conclusions

The influence of environmental factors on the abundance and distribution of Cape hake species needs further study. The Orange Banks on the west coast of the southern Benguela is a suitable nursery ground for deep-water Cape hake juveniles. Analyses of selected environmental variables indicate that near-bottom oxygen concentrations could have an influence on the distribution and abundance of deep-water Cape hake juveniles, more so than temperature and salinity. However, temperature, salinity and oxygen are not the only environmental variables influencing hake abundance along the west coast of the southern Benguela; winds are also important. Future studies should relate seasonal wind speeds with seasonal recruitment estimates and spawning-biomass in the same years to understand whether Cape hake spawners or recruits or both are favoured by strong winds. In addition, the relationship between winds and bottom oxygen concentrations needs further study.

Chapter 4: Conclusions and Recommendations

Environmental variables influence spatial and temporal patterns of fish spawning and recruitment. Variability in spawning times and duration in the life cycles of fish species found off Norway and South Africa were investigated in relation to environmental conditions (Chapter 2). Spawning times and duration can vary depending on habitat selectivity and preferred environmental conditions in the South African coastal upwelling ecosystem. The small pelagic fishes (anchovy, sardine, round herring and Cape horse mackerel) spawning off the South African coast have timing and duration that showed a lot of shifting temporal patterns compared to the demersal fishes (Cape hakes). Some of these conclusions may be biased as the data sources had unequal spatial coverage during data collection or varied in time scales. In contrast, the spawning times and duration patterns of Norwegian fish species showed extreme restriction of spawning season and timing and did not last long for both small pelagic and demersal fish species. There was not much variability involved.

It is assumed that the oceanographic dynamics involved in the coastal spawning region in Norway's high latitude marine environment have strong seasonality, which determines these patterns. A dominant environmental signal assumed to be associated with the spawning timing and duration off the South African coast is the short-term variability/intra-seasonal variability in oceanographic conditions influenced by the strength of upwelling favourable winds (south-easterlies), highly dynamic productivity (nutrient-rich waters) and thermal stabilities. This is completely different to spawning that occurs off the Norwegian coast, as inter-annual differences were observed in spawning times and duration, assumed to be due to strong seasonal variability in oceanographic conditions influenced by down-welling favourable winds (south-westerly), light regime intensity for phytoplankton growth and salinity gradients. This does not mean other signals do not play an important role in influencing spawning times; it implies they are the dominant ones.

The comparison between the Norwegian small pelagic and demersal fish spawning shows not much difference in time and duration, although intensities may differ. This implies that, besides the effect of environmental factors, prey-predator interactions may play a role.

The findings of chapter 3 showed that the distribution and abundance of deep-water Cape hake juveniles could possibly be associated with near-bottom oxygen concentrations and wind speed. The findings indicate that the relationship between wind speed anomalies in summer (Lag = 0 years) and autumn (Lag = 1 year) were statistically significant for this species, with high recruitment success. Near-bottom oxygen variability showed a dominant effect on the distribution of Cape hake juveniles on their nursery areas. Small-sized deep-water hake juveniles were observed to occur more frequently than expected in near-bottom waters that were oxygen-depleted. Medium-sized deep-water Cape hake (> 16 cm) were scarce in hypoxic near-bottom water and large-sized fish occurred more frequently than expected in oxygenated waters. Other environmental factors that could possibly play a role in distribution of both Cape hakes are near-bottom temperatures and salinity. The intra-seasonal variability observed in temperature and salinity maps indicate changes in the mid-inner shelf near-bottom waters but not for the outer shelf. Upwelling could lead to short-term variability by influencing thermal stabilities. During these demersal surveys, the distribution maps show enhanced catches of deep-water hake juveniles off the Orange Banks and Cape Peninsula, but reduced catches off Cape Columbine. The Orange Banks is confirmed here to be a primary recruitment area for juveniles (length size < 16 cm) of deep-water Cape hake. This does not imply that these juveniles do not use other nursery areas on the west coast. This study analyses data that have some limitations, which possibly introduced some biases. Understanding the role of oceanographic variability in recruitment success off the west coast remain a problem requiring further study.

In order to test the results presented here and to predict patterns that might be expected in the future, climate proxies combined with trophic effects can be used to create a model that links physics and trophic dynamics to fish life cycles. It would be useful to include intra-annual events spanning life history stages. The patterns of intensity and timing of upwelling favourable winds probably influence recruitment and retention of deep-water hake juveniles, although the detailed mechanisms remain unclear and further information about *Merluccius capensis* should be sought.

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APPENDICES

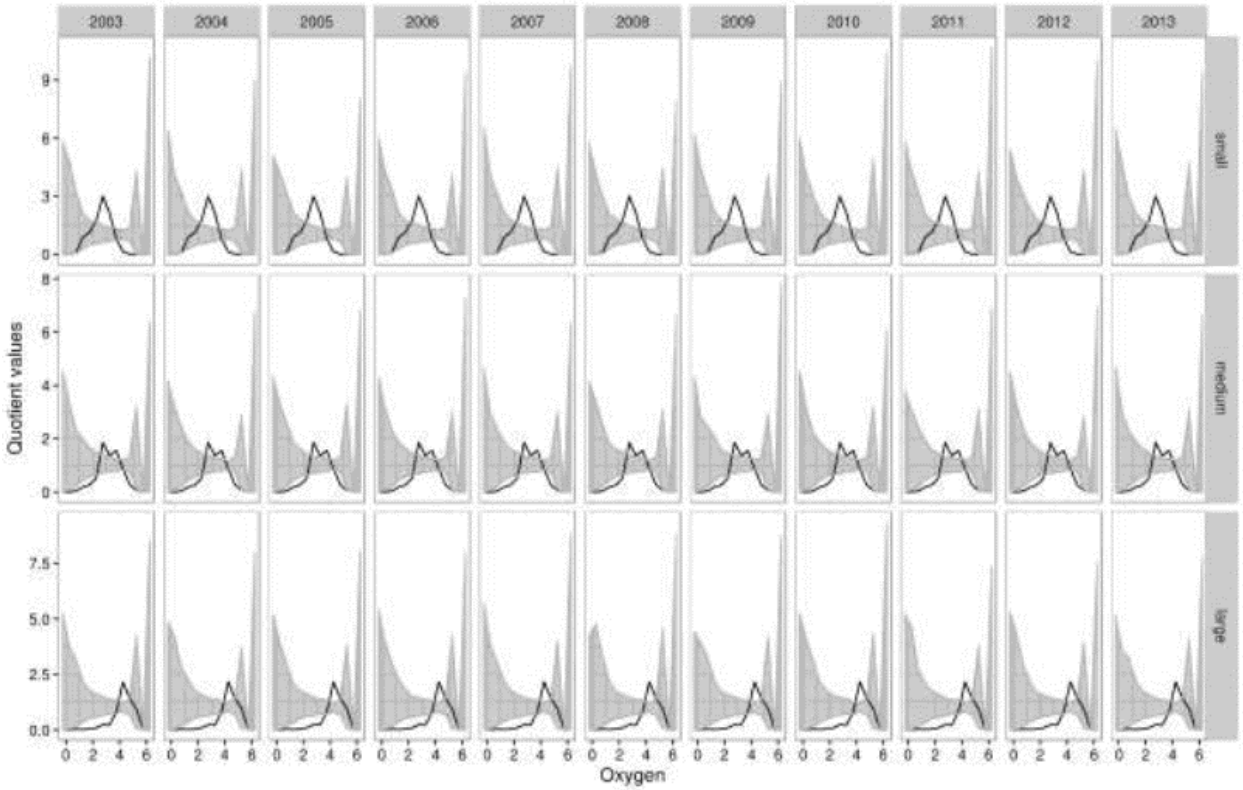

Figure A1: Time series of frequency distribution of near-bottom oxygen for all Nansen surveys from 2003 – 2013 and quotient curves (solid lines) for deep-water Cape hake for different length class ranges: (a) small (0-15 cm), (b) medium (22 – 35 cm) and large (36 – 50 cm).

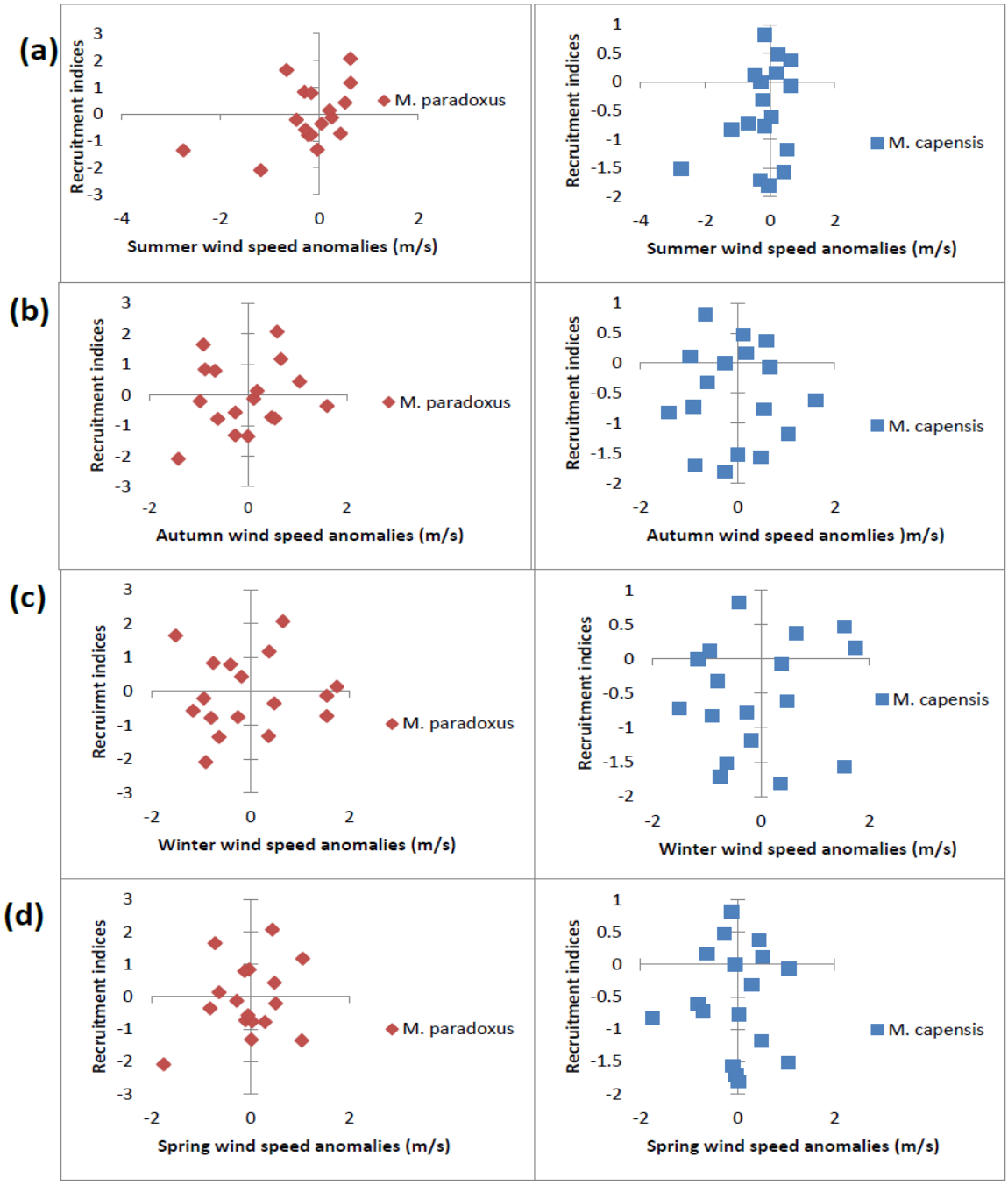

Figure A2: Scatterplots showing the relationship between recruitment of two Cape hake species and average yearly wind speed anomaly of each season: (a) summer, (b) autumn, (c) winter and (d) spring.